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# A TREATISE ON ZOOLOGY

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# TREATISE ON ZOOLOGY

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## PART I

## INTRODUCTION AND PROTOZOA

### SECOND FASCICLE

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# PREFACE TO SECOND FASCICLE OF PART I.

## INTRODUCTION AND PROTOZOA

THE irregular publication of the parts of the *Treatise on Zoology* is the inevitable result of the fact that it is the work of a number of authors.

I have determined not to allow Professor Minchin's most timely and valuable treatise on the Sporozoa to lie by in the printers' hands until the other sections of Part I. which logically precede it are ready for the press; and with this I have been able to combine Dr. J. J. Lister's section on Foraminifera (which contains much that is new and original), Professor Hickson's section on Infusoria, and a section on the Structure of Animal and Vegetable Cells, with especial reference to the points which arise in the study of the Protozoa, by Professor Farmer.

These four sections form the second fascicle of the First Part of this treatise; the first fascicle, which is in preparation, will contain an Introduction and descriptions of the Proteomyxa, Mycetozoa, Lobosa, Heliozoa, Labyrinthulidea, Radiolaria, and Flagellata, forming sections A to G of Chapter I.—The Protozoa.

The division of the work into Chapters, of which the second to the twenty-first are already published, has resulted in a somewhat awkward restriction of the Protozoa to nominally one chapter, the first. This unduly large chapter is broken up into sections which serve instead of the usual division of so large a number of pages into chapters. The parts of the *Treatise on Zoology* dealing with the Mollusca, the Arthropoda, and the Vertebrata are in active preparation.

E. RAY LANKESTER.

*May* 15, 1903.

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# CHAPTER I.—PROTOZOA (*continued*)

## SECTION H.—THE STRUCTURE OF ANIMAL AND VEGETABLE CELLS[1]

In reviewing the course of development of our knowledge of organic nature, there stands out one epoch-making discovery, that of the chambered structure of plants, made by Hooke in 1665, which was destined not only to profoundly modify the older conceptions as to the intimate organisation of animals and plants, but also to place in clear relief the fundamental unity which underlies the apparently endless variety of external form. But, as in the case of most discoveries of wide-reaching import, the general recognition of the true nature of the cell did not emerge at once in its modern form, nor was it in reality the outcome of the work of any single investigator. Indeed, nearly two hundred years elapsed before the first enunciation of the doctrine of a cellular structure of plants

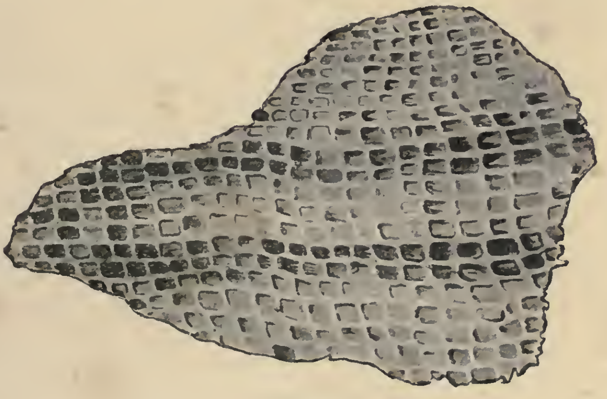

Fig. 1.

**Facsimile of part of a figure by Hooke representing cells of vegetable tissues (cork).**

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[1] By J. B. Farmer, D.Sc., M.A., F.R.S. (1902).

by Hooke became translated into a form comparable to that in which the phrase is now understood.

Nevertheless to Hooke belongs the credit of having not only depicted the vesicular nature of cork and other plant-structures, but also of having designated the cavities by the name of cells.

Malpighi and Grew in the succeeding century had fully recognised the cellular character of plants, and even attempted a crude explanation of the origin of the cells themselves, likening them to the vesicular foam of beer. But accurate as was their portrayal of the mature structure, they nevertheless possessed no real conception of the true meaning of the cell as the unit of organic life. The cells were regarded as the cavities in the matrix, not as the units which together constitute the organism, and it was to the *wall* that all their observations were directed. Little or no attention was seriously paid to the cell-contents. Thus, although Corti in 1772 had noticed the rotation of the viscous matter in the cells of Chara, his discovery remained without influence, and was made again, and independently, by Treviranus some forty years later. Even the discovery[1] of the nucleus by R. Brown in 1831-33 failed at once to excite the interest of the majority of his contemporaries, nor indeed does it appear that Brown himself at all fully grasped the significance of his discovery. Whilst in the plant-body it was the cellular structure, in the sense of Hooke, Malpighi, and Grew, which most forcibly appealed to the observer, the softer tissues composing an animal body were not so easily referable to a similar plan, although a consideration of the blood corpuscles, and of cartilage, helped to pave the way for the later generalisation. But, on the other hand, the animal body was more suited to turn the attention of the investigator upon the living substance, and the fundamental importance of the latter seems to have been first clearly apprehended by Dujardin, who (in 1835), gave the name of Sarcode to the contractile, gelatinous, diaphanous mass constituting the bodies of the Infusoria which he was examining. He even succeeded in distinguishing some structural details, but with the lens at his command it may perhaps be doubted whether this really represented more than the arrangement of granular and other inclusions in the living substance.

It was, however, chiefly due to the researches of Schleiden, and especially of Schwann, which were published in 1837-38, that general interest became steadily focussed upon the cell-contents, including the nucleus which formed a cardinal point in their famous cell-theory. And it is largely to the great influence exerted by their work that the rapid advances witnessed during the next succeeding decades are legitimately to be traced. It is, of course, true that the greater part of their conclusions, especially such as are related to the genesis and growth of cells, have since turned out to have been erroneous. This is largely due, perhaps, to the weight of mistaken preconceptions on their part; but the history of advance in any line of thought or science is full of similar examples. It is sufficient that they realised to the full the immense importance of the inquiry, and at any rate they succeeded in correlating and in co-ordinating a large mass of observations, and so became the means of immediately attracting numerous other workers into the same field.

---

[1] Others, including Leewenhoeck, had already seen nuclei in isolated cases, but their observations were quite without influence on the development of thought.

To Schwann may be conceded the merit of having first consciously attempted to demonstrate, in the most effective manner, the essentially similar character of the cells in plants and animals. This he did by endeavouring to follow out the origin and development of new cells in each of the two great divisions of living organisms, though how wide he was of the practical truth may be seen from the account which he gives of the process. The primordial substance out of which cells are formed consists, according to him, of a gelatinous or slimy mother-liquor, the *cytoblastema*. In this, by a process of condensation, a nucleolus is first formed. This then grows by intussusception, and gives rise to a nucleus, in which once more a nucleolus is differentiated—itself the origin of another nucleus. Meantime, from the cytoblastema fresh matter is deposited in the surface of the nucleus, and thus a consolidated membrane originates. This membrane, by intercalation of constantly increasing material within it, continues to grow, and ultimately it forms the wall of the new cell, the contents of which are provided for in the way just described. Thus, in the formation of cells, according to Schwann, the following stages, starting from the raw material—cytoblastema—may be distinguished. First, the condensation giving rise to the nucleolus, this in turn, by growth, produces the nucleus, and the peripheral (nuclear) wall eventually forms the wall of the new cell. At first sight it is difficult to realise how these ideas obtained the wide currency which they enjoyed, but the reason is to be sought in the fact that Schwann, like Schleiden and Nägeli after him, was not fortunate in the material he selected for investigation. Cartilage, blood-corpuscles, and pollen grains were repeatedly studied, and it is perhaps not surprising that with such objects before them an incorrect conclusion was arrived at.

Von Mohl, who had been engaged in studying the structure and mode of division of vegetable cells since 1835, at one time gave a true explanation of the process, but afterwards he sounded a less certain note, adhering to the view that the new cells were formed *in toto* within the mother cells, even in the case of algal filaments—an error which was definitely opposed by Unger. Von Mohl clearly recognised the importance of the formative substance of the cell, to which in 1846 he gave the name it now bears, viz. Protoplasm, the same word that had already been employed six years earlier by Pŭrkinje to designate the formative substance met with in the animal embryo.

Speculation was already aroused as to the possibility of instituting a comparison between vegetable protoplasm and animal sarcode, and Dutrochet had, as early as 1824, and still more definitely in 1837, indicated the general similarity which underlies the structure of animals and plants. But it was reserved for Cohn to clearly formulate in 1853 the real features of identity between them, and to express the definitely reasoned view that they were, in all essentials, composed of the same kind of substance. Cohn was well fitted for the task, by his acquaintance with the lower organisms of both animal and vegetable kingdoms. Max Schultze in 1861 further elaborated this resemblance, and his convincing demonstration at once gained the assent of all who were competent to form an opinion on the question. Moreover, Schultze clearly saw that it is the protoplasm (in the widest sense of the term) which essentially constitutes a cell, and he, like Leydig, defined it as a mass of protoplasm containing a nucleus. About the same time also Virchow, in his celebrated aphorism, "Omnis cellula e cellulâ," crystallised the correct view as to the general mode of origin of new cells.

But although the essential facts of cell-structure and development thus gradually emerged from the earlier and cruder notions, the finer details, and especially the relations of the nucleus, long remained obscure. The origin of this body, and its connection with the rest of the cell-contents, was not understood, and a very general view was held that it disappeared (as indeed is in a certain sense correct) at each cell-division, to be formed afresh in the new daughter cells. It is true that so long ago as 1841 Remak had put forward the statement that the nucleolus and nucleus gave rise by direct fission to the corresponding structures in the daughter cells, and indeed that the whole process of cell-division was thus inaugurated; but his views (which for a few cases are really well founded) appeared to be not generally applicable, and thus it transpired that even in the middle of the century the nucleus came to be commonly regarded as an organ of but secondary importance, and this even by so eminent an investigator as Brücke. It was not until the publication of Strasburger's magnificent work on the cell- and nuclear-division in 1875 that the nucleus received its proper share of attention. Strasburger, some four years later, like Virchow, in another connection, before him, defined the modern position in the phrase "Omnis nucleus e nucleo." The researches of the brothers Hertwig, Van Beneden, Flemming, and others have abundantly emphasised and justified these far-reaching generalisations.

But with the improvements which have been effected in technique during the last quarter of a century, new facts have come to light which have somewhat modified the conception of the cell as held by the earlier writers. It has been already seen how the centre of gravity gradually shifted from the cell-wall to the cell-contents, and that, as Max Schultze declared, the essential constituents of the cell were represented by the protoplasm and the nucleus, the wall being of altogether subordinate importance. The discovery that masses of protoplasm might contain not one but many nuclei, and that such a condition is not uncommon both amongst various groups and tissues in plants and animals, appeared to some writers to present a difficulty in accepting the cell theory as treated above, and various explanations have been offered in order to bring these cases into line with the theory as more generally understood and defined. Such organisms or tissues have been termed non-cellular—a negative and unsatisfactory expression which has been replaced by the more appropriate word *syncytium* or *coenocyte*. These words emphasise the view that, morphologically, the individual units, which collectively make up the syncytial tissue, are not isolated from each other by definite barriers. Sachs proposed the term *energid* to express the cell in Max Schultze's sense, meaning thereby the nucleus, together with the portion of protoplasm dominated by it. Essentially this is a physiological definition as contrasted with the morphological idea embodied in the word *syncytium*. And it is, on the whole, a legitimate expression, since it really does correspond to a fact. Moreover, it has the merit of being equally applicable to the cases of isolated cells as well as of those in which such limits are not structurally traceable. The objection raised to the conception underlying it, on the ground that the nucleus of a syncytium does not always dominate the same protoplasm, is not a valid one, inasmuch as it is quite possible—perhaps even probable—that an essentially similar state of things also obtains even in those tissues in which the constituent cells are apparently isolated. For it has gradually been proved for a very large number of cases that the protoplasm of adjacent cells is in actual physical continuity through the fine pores present in the delimiting cell-walls. It is tolerably easy to observe this continuity in the epithelial cells of some amphibian tissues, and there is a considerable weight of evidence to show that it is far more general than was generally supposed to be the case. In plant-tissues also it has been repeatedly demonstrated since its first discovery by Tangl (in 1879) in the endosperm of certain seeds. Gardiner and Russow almost simultaneously demonstrated its existence in the tissues of several adult plants in 1883, and since that time it has been clearly proved to occur throughout the tissues of the organism in those examples which have been specially investigated for the purpose. Thus it is evident that, so far from the syncytial condition presenting an exceptional case, it is in reality an extremely common one, the cell-walls merely forming a perforated skeletal framework which supports the softer parts. It is useless to argue (as has recently been done) that the pores are so fine as to be practically useless for the transference of material substances through them, since, as Horace Brown has shown, their very narrowness, taken together with the thinness of the portion of membrane on which they occur, is an important condition for the performance of such a function without unduly weakening the framework itself. Moreover, the existence of the continuity of the protoplasm from cavity to cavity at once renders intelligible the possibility of a transmission of stimuli from one part of the body to another, although it would perhaps be going too far to assume this as a necessary condition of transmission. Examples are known in which the stimuli appear to be less directly conveyed, as, for instance, in the case of nerve ganglia, according to Ramon y Cajal (although his results have not been upheld by some other investigators); and further, in some plant tissues, water squeezed out into the intercellular spaces has been regarded (on rather slender grounds) as being the means of exciting consecutive cells of a tissue. On the other hand, Němec has recently shown reason for admitting, in the irritable parts of plants, the existence of specialised tracts of protoplasm which are continuous from cell to cell, and by the agency of which the stimulant impulse is conveyed to the motor executive region. Whilst the general and mutual relations of the constituent parts of the cells were being gradually elucidated, it became recognised that the cell-substances themselves were not composed of

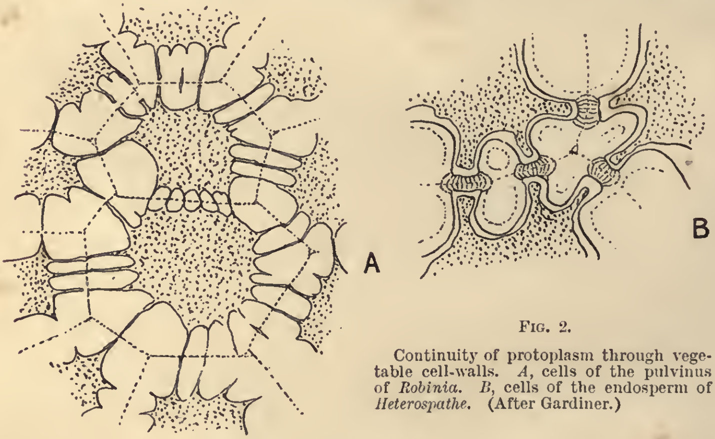

Fig. 2.

Continuity of protoplasm through vegetable cell-walls. *A*, cells of the pulvinus of *Robinia*. *B*, cells of the endosperm of *Heterospathe*. (After Gardiner.)

mere structureless jelly, but possessed an organisation of their own. At first the recognition of this fact only appears in tentative suggestions, and hardly any serious progress was made beyond the obvious distinction of the nucleus from the protoplasm. Brücke seems to have been the first to point out the philosophical necessity of assuming an organisation in the protoplasm, but the visual perception of the counterpart of such a constitution hardly advanced beyond the recognition of a relatively solid mass bathed in a more fluid substance. The former was distinguished as spongioplasm, and the latter as hyaloplasm. It is significant of the difficulty experienced in arriving at a definite decision on the then available evidence that each of the two constituents has been claimed by different writers as the living substance.

The views which have been put forward as to the relationships of the various substances which co-exist in the protoplasm to each other have developed in two principal directions. The earlier, historically speaking, was advocated by Frommann in a series of papers dating from 1864. He was led, by a study of nerves, to distinguish a reticulum, which partly corresponds with Leydig's spongioplasm. This reticulum was imbedded in a more homogeneous ground substance, which, however, includes much more than spongioplasm. He extended this conception of protoplasmic structure to plant cells, and it was utilised, and in some respects modified, by Heitzmann in 1873. The views of the latter author were not so convincing as those of Frommann, for it is quite possible to identify the structures described by the latter writer in living cells, although the appearances are susceptible of a different interpretation from that given by him. Heitzmann's descriptions, on the other hand, are very schematic, and it is difficult to avoid the conviction that they are highly coloured by theoretical preconceptions. The phenomena of contraction and extension were brought by him in relation to the structures as described, but his views have never met with very general acceptance. A closely related hypothesis was that suggested by Flemming, who, while denying the existence of a reticulum, insisted on the presence of a fibrillar structure, the fibrils being represented as threads of irregular length (the filar elements) which were imbedded in a more fluid interfilar mass.

Gradually another view of the structure of protoplasm was evolved, and which, in a measure, took account of reticular structure, but explained it differently. Strasburger in 1876 first seems to have spoken of closed protoplasmic chambers, which were filled with more fluid albumen, but he soon abandoned the idea in favour of the reticular hypothesis. But the alveolar theory thus indicated was developed and extended by Bütschli, who had, as long ago as 1873, figured in Pilidium a structure susceptible of such an explanation, though this was not given at that time. The alveolar theory has exerted considerable influence upon contemporary thought, and may be given in brief outline. The whole protoplasm, including the nucleus, is conceived of as in a physical condition resembling an emulsion, the more fluid mass filling the cavities (which are very small, 1-2 $\mu$ in diameter), whilst the walls are composed of a more viscous substance. Such an emulsion obeys certain well-known physical laws, and the relation of the alveolar walls both to each other and to the free outer surface can be theoretically defined. Solid heterogeneous particles enclosed in the emulsion, if too large to lie in the substance of the walls, are surrounded by a surface film in which the alveoli are arranged, as they also are on the free surface, somewhat like the cells of columnar epithelium. Movements may occur in the whole mass, as the result of disturbances in the surface tension of the superficial alveoli, and movements produced in emulsions in this way closely resemble the streaming and other movements of protoplasm. The reticular and filar appearances are also to be attributed to disturbances, due to causes, in the interrelation of the alveoli, or they may represent the optical section of the alveolar walls themselves.

Now it is quite possible to convince oneself that such an alveolar structure does actually exist in many cases, although, as Bütschli himself admits, it is not always to be so identified. It seems probable, however, that on the whole it does represent truly the appearance of protoplasm under certain (and commonly occurring) conditions, but it also seems equally clear that these conditions are not necessarily always fulfilled. For it is essential for the production of such an appearance that there shall be at least two non-miscible fluids of different refractive index, and if either of these conditions is not realised, or is temporarily in abeyance, it will follow that the alveolar appearance must also be absent or disappear. And we are acquainted with so many important series of changes in the relations of the various protoplasmic constituents to each other that it is hardly necessary to postulate the permanence of those conditions of which an alveolar structure is the consequence. Thus it would seem that an easy *modus vivendi* might be reached which would render it possible, whilst recognising the heterogeneity of the substances included under the generic term Protoplasm, to admit that at one time an alveolar, at another a filar, or a reticular appearance might occur. A fibrillar structure is certainly present during nuclear division, and although the extreme adherents of the

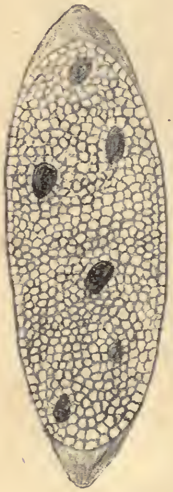

FIG. 3.

The foam structure of the protoplasm of a gregarine.

alveolar theory see in the fibrils a honeycomb structure, the cavities are generally admitted to be reduced to the vanishing point.

Strasburger has attempted to utilise both the filar and the alveolar hypothesis, considering that in every cell the protoplasm outside the nucleus consists of two distinct parts. The one, which is specially nutritive and alveolar, he terms *Trophoplasm;* the other, which is more closely concerned with the dynamical changes in the cell, and possesses a filar structure, he designates as *Kinoplasm.* The relations of the kinoplasm will be more specially considered in connection with nuclear division.

Besides the protoplasm and nucleus, there are present other organised structures in the cell. The vacuoles, which have long been recognised, are cavities in the protoplasm, and lined apparently with a specialised layer of this substance. In some cases they are rhythmically contractile as in many of the Protozoa.

But it is around that enigmatical body, the centrosome, that especial interest has persistently attached ever since its first definite discovery by Van Beneden in 1885. The centrosomes are minute granules, most often situated either singly or in pairs in each cell, and in close proximity to the nucleus. They are frequently contained in a specialised mass of protoplasm, termed by Boveri the *Archoplasm.*

Centrosomes and their attendant structures have been differently described by various observers. Van Beneden, to whom we owe the first recognition of these bodies, distinguished, in the case of Ascaris, a central granule, surrounded by two concentric areas, to which he gave the names of medullary and cortical zones respectively. Boveri described in the cells of the same animal a centrosome surrounded by a lighter zone, from which it was definitely cut off by a kind of limiting membrane. Within the centrosome he further distinguished a central granule, the centriole. The latter body divides before the centrosome increases by fission.

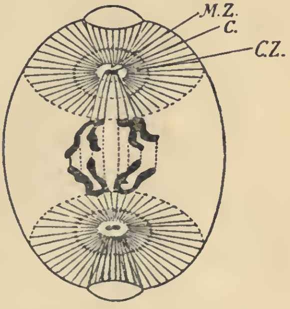

Fig. 4.

*Ascaris megalocephala.* Schematic figure of diaster stage of the first cleavage mitosis. *c*, centrosome; *m.z*, medullary zone; *c.z*, cortical zone. (After Van Beneden.)

In still other cases (*e.g.* in cells of the testis of Salamander) various observers (Meves, Drüner, etc.) have distinguished a whole series of concentric zones around the centrosome. In the giant cells of the spinal cord and in leucocytes, Heidenhain has distinguished a group of granules, which replace the single or paired one more commonly met with, and in other cases again there is a reticulate sphere (echinoderms) containing a varying number of granular inclusions. In plant cells centrosomes have been far less often identified than in animals. They are more frequent, or at least more easily demonstrable, in the lower members of the vegetable kingdom than in the higher plants, in which they are probably restricted to the motile sperms. The evidence for their occurrence in angiosperms is not convincing. When present in a cell, they usually occur in the form of a small granule enclosed in a sphere, and are comparable with the centrosome and centriole of Boveri. Strasburger has proposed the convenient term of centrosphere to designate the sphere together with its included granule, reserving the term centrosome for the latter body only. It is quite certain that the centrosphere apparatus presents itself in varied degrees of complexity, not only in different organisms, but even in different cells of the same tissues, and Strasburger's term has much to recommend it, since, in spite of the large literature which has grown up around the subject, we are still mainly in the dark as to the true meaning and relations of the different parts. It seems clear, for example, that the centriole of Boveri corresponds to that which by most writers has been called the centrosome, and Boveri himself states that the division of his "centrosome" is preceded by that of the centriole.

The centrosome or centrosphere is itself not unfrequently enclosed in a denser mass of protoplasm, called by Boveri the Archoplasm, and by Strasburger the Kinoplasm. Probably, however, appearances denoted by these terms are not the expressions of permanent structures, but represent transient phases of cellular activity. The structures thus called into existence may, however, be, at least temporarily, very pronounced, since at least a part of the achromatic figure, which is formed during nuclear division, owes its origin to the archoplasmic mass. Nevertheless, the archoplasm (or kinoplasm) may become absolutely indistinguishable at other periods in the life of the cell.

A far more difficult question to answer than that concerned with the permanence of the archoplasmic or kinoplasmic structures refers to the centrosome itself in a similar connection. Whilst many authors have strenuously maintained its permanence from one cell-generation to another, comparing it in this respect with the nucleus itself, a considerable weight of negative evidence has nevertheless accumulated in the opposite scale. The striking relations which obtain between the centrosome and the nuclear figures at phases of division naturally produce a profound subjective impression upon the observer, and it has even been assumed that the centrosome still persists, even when its actual existence cannot be successfully demonstrated. There is no doubt that other granules have frequently been mistaken for centrosomes, selected because they happened to lie sufficiently near the spot where the structures in question might have been looked for, and thus no little confusion has been introduced into a subject already sufficiently bristling with difficulty. But the cases of Acanthocystis (Schaudinn) and of Actinosphaerium (R. Hertwig) show quite clearly that centrosomes may, at least in the lower animals, be certainly differentiated afresh in the cells from which they had previously been absent.

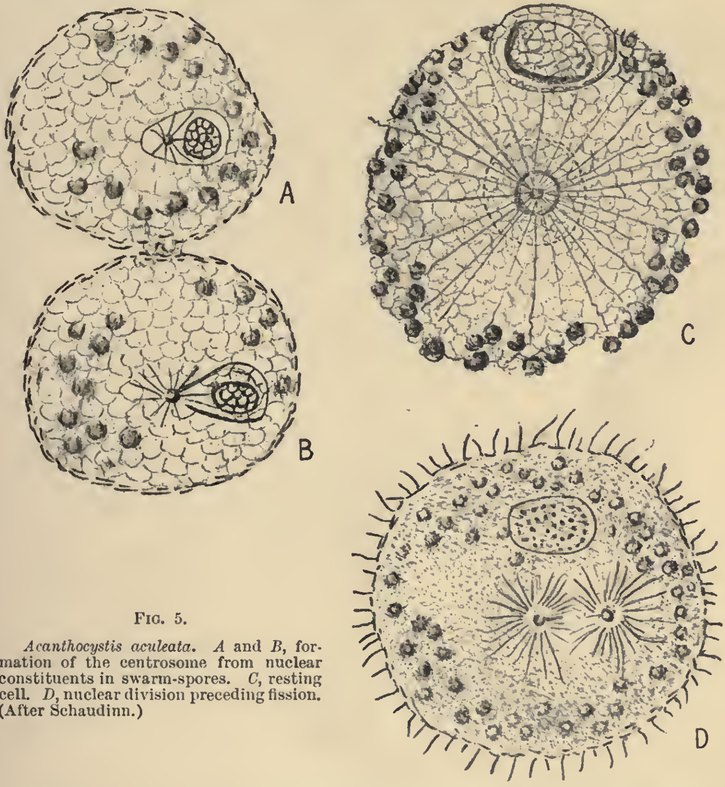

FIG. 5.

*Acanthocystis aculeata.* *A* and *B*, formation of the centrosome from nuclear constituents in swarm-spores. *C*, resting cell. *D*, nuclear division preceding fission. (After Schaudinn.)

The so-called Blepharoplast, which is associated with the male reproductive cells of certain cycads and ferns, appears to present very strong analogies with animal centrosomes, and yet the blepharoplasts have not been seen in the antecedent cell-generations of the plants in which they occur, and hence they have almost certainly been formed *de novo.* On the whole, then, the question as to the relative permanence of the centrosomes through the series of ontogenetic cell-generations must be left an open one. Certain facts are, however, known which conclusively prove that centrosome-like structures can be formed in cells from which, under normal circumstances, they are absent. Morgan showed that concentrated solutions of salts could induce the appearance of centrospheres with radiations in the eggs of certain echinoderms, and Loeb further proved that by adding magnesium chloride in appropriate quantity to sea-water, the eggs of sea-urchins could be brought into such a state that when replaced in normal salt water they underwent the normal embryonic segmentation. Wilson, investigating the cytology of the process, confirmed the results, and ascertained that the treatment caused the formation of centrospheres which seemed to direct the cell-divisions. And R. Hertwig long ago showed that at least the early stages of a parthenogenetic segmentation could be similarly induced by the action of strychnine. Hence there is a considerable body of evidence to show that the centrosomes are structures which, though physiologically the signs

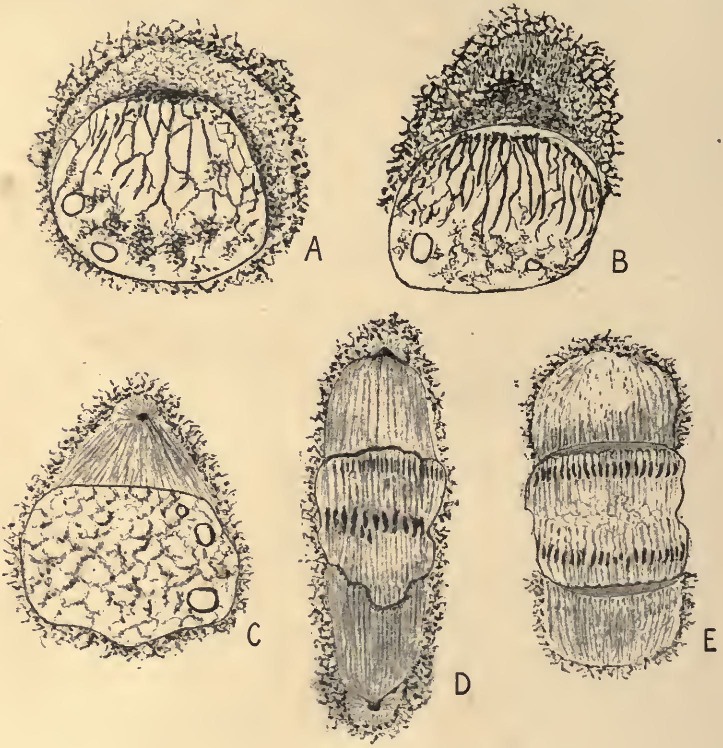

Fig. 6.

*Actinosphaerium eichornii.* *A* and *B*, nuclear origin of the centrosome, which arises at one end of the nucleus. *C*, *D*, further stages in the mitosis (*A-D* refer to the first polar mitosis). *E*, diaster of a somatic mitosis, in which no centrosome is present. (After R. Hertwig.)

of important changes in the protoplasm, are not necessarily permanent organs of the cell. And a wide survey of the processes of mitosis in the lower animals and plants serves fully to confirm this conclusion.

### *The Structure of the Resting Nucleus.*

It has already been said that it was not until the year 1875 that the nucleus was fully and universally recognised as an all-important cell organ. Even as late as the previous year, Auerbach published a treatise on its behaviour during cell-division maintaining that it completely disappeared during the process, and he gave the name of Karyolysis to the phenomenon in question. With the recognition of the complex series of changes undergone by the nucleus during division, and its obvious importance, in connection with fertilisation, also discovered in 1875, it speedily formed an object of serious study. And the investigations were not only carried on in killed cells, but its behaviour during life, as well as its chemical structure, presented attractive problems for solution. The general outcome of these investigations is as follows:—The nucleus is delimited from the cell protoplasm (the cytoplasm of Van Bambeke) by a membrane which was regarded by Schwartz as consisting of a substance called by him Amphipyrenin. In some cases, however, it appears not improbable that the membrane is at least partly produced from the cytoplasm, as a kind of precipitation membrane, whilst in other cases, as for example in some of the coccidia, Schaudinn has shown grounds for thinking that the so-called chromatin of the nucleus itself may contribute to its formation.

Within the membrane the nuclear contents may be distinguished as a matrix of a substance which stains with some difficulty, and which forms a sort of meshwork within it. This is the Linin of Schwartz, and seems to closely correspond with the plastin, distinguished chemically by Zacharias. In addition to the linin there exists a more fluid gelatinous substance, the Paralinin of Schwartz. Imbedded in the linin are a large number of granules which, by reason of their exhibiting a strong affinity for certain dyes, were termed Chromatin by Flemming. The chromatin consists of a highly complex nitrogenous substance, and always contains phosphorus. Chemically it belongs to the class of proteid compounds classed as nucleins, and by analysis can be made to yield proteids and nucleic acid. In addition to the true nuclein chromatin, there have been described other inclusions within the linin known as Lanthanin (Heidenhain) or oxy- or basi-chromatin bodies, which appear to be related to the nuclein series, and which perhaps are complex, high-graded substances which can be built still further up to true nucleins.

Most nuclei contain, besides these constituents, one or more masses, usually of a spherical or oval shape, known as Nucleoli. These bodies long ago attracted the attention of investigators, and it will be remembered that they were raised to a rank of considerable importance by both Schwann and Remak. They usually are easily stained, and thus were included amongst the chromatin bodies of the nucleus, but subsequent investigation has shown that they are, in many cases, widely different from nuclein. Two kinds of nucleoli were distinguished by Flemming under the names of eu- and pseudo-nucleoli respectively, the latter representing, at least chiefly, aggregations of a substance which closely approximates to, if it is not actually identical with, true nuclein. And more recent investigations have tended to confirm the supposition advocated by Zacharias, that the ordinary eu-nucleoli, so far from consisting of a single substance such as pyrenin (Schwartz), are complex mixtures, or else, at any rate, bodies which readily yield, by suitable treatment, different substances of complex molecular composition. It is true that the author just referred to arrived at the conclusion that the nucleoli were destitute of phosphorus, but this view can hardly be maintained, at least in all cases.

Investigations on the nuclei of Protozoa and of some of the lower plants seem to have shown that these nucleoli consist of at least two groups of substances, the one consisting of, or approximating to, nuclein, the other more nearly resembling the linin, or even the cytoplasm, in its staining and other reactions. At any rate, the chromatin, which forms so obvious a character in dividing nuclei, appears in some cases, *e.g.* Actinosphaerium, to be mainly derived from a nucleolar source. It is highly probable that these bodies are really heterogeneous, and represent reserves of complex materials which can be drawn on for various purposes during periods of nuclear activity. For at such times the nucleolus always undergoes considerable change, and is either completely used up, or its remains fragment and pass out into the cytoplasm, where their further fate is still obscure.

Whilst the nucleoli are thus losing substance they often exhibit vacuolation, and even in resting nuclei vacuoles may sometimes be detected within the nucleoli, pointing strongly to the correctness of the hypothesis as to their heterogeneous nature.

A further point which deserves mention in connection with the nucleoli is the view held by some writers (*e.g.* R. Hertwig) that they stand in some close relation to the centrosomes, and that the existence of the latter structures may be traced back to a nucleolar origin. Further, Strasburger, in his account of kinoplasm, has suggested that the nucleolar substance may serve as the material which stirs up the dynamical and metabolic activities latent in the cell. On the whole, it is impossible, in the present state of our knowledge, to ascribe any single function to these bodies, and the evidence before us seems to indicate that just as they are very diverse in structure and composition, so also they may, and almost certainly do, play very different parts in the general economy of the cytoplasm and nucleus.

The resting nucleus may, then, be regarded as an organised structure containing a considerable assortment of highly complex and labile substances. But this very lability, itself a condition of the profound and important changes which succeed each other with extraordinary rapidity during the division of a nucleus, is bound up in, or at least is related to, an organisation which directs and determines that sequence of chemical and physical transformations which so strikingly accompany the whole process. Moreover, there is abundant evidence of the existence of a material exchange passing between the nucleus and the cytoplasm which becomes strongly marked at all periods of special cellular activity—such, for example, as secretion, regeneration, and the like.

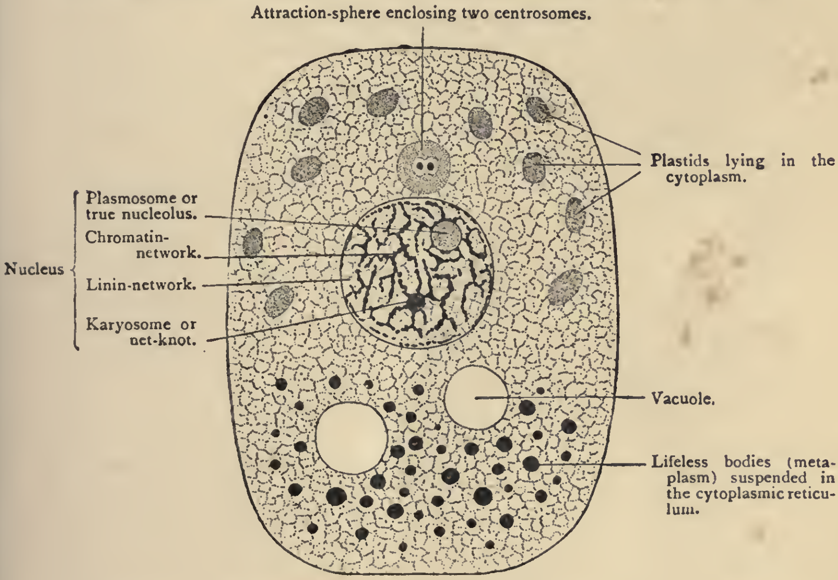
Attraction-sphere enclosing two centrosomes.
Plastids lying in the cytoplasm.
Nucleus
Plasmosome or true nucleolus.
Chromatin-network.
Linin-network.
Karyosome or net-knot.
Vacuole.
Lifeless bodies (metaplasm) suspended in the cytoplasmic reticulum.

FIG. 7.

Diagrammatic representation of the structures present in a typical cell. (After Wilson.)

### *Nuclear and Cell Division.*

The multiplication of the uninucleate cell is always preceded, save in the lowest protozoa and protophyta, in which the details of the processes are still obscure owing to the absence from them of a well-defined nuclear body, by a division of the nucleus. This may either take place in a simple manner, as was determined by Remak, or it may only be secured as the result of a complicated rearrangement and fission of certain nuclear constituents. To the former, or *direct* (Flemming), method of division, the term Amitosis has been applied by Flemming, whilst the latter, or *indirect* (Flemming), method was also termed Mitosis by the same author. The word Karyokinesis (Schleicher) has often been substituted for mitosis, but both terms are expressive of the same phenomena. Amitosis, in the higher animals, is not of such generally widespread occurrence, but in the lower forms it frequently appears as an intercalated method along with a more or less complex form of ordinary karyokinesis. It is also generally met with in nutritive gland cells; thus in the follicular epithelium of the ovary, in the "foot" cells of the testis, and in the tapetal cells of the higher plants, it is not uncommon. In these cases it appears to be characteristic of degenerating tissues, and this explanation has been extended to amitosis generally by Ziegler and vom Rath, but many instances are known in which such a view is quite untenable. Thus, there is good reason to believe, as Meves or others have shown, that in the ovary, cells which ultimately are destined to give rise to ova may multiply in this way, and Schaudinn, Siedlecki, and others have shown that in the Sporozoa such amitotic divisions often follow shortly on the act of fertilisation, and give rise directly to the new generation of parasites, and again amongst Infusoria the macronucleus seems always to increase in this way. Furthermore, Nathansohn proved, in the case of Spirogyra, that by appropriate treatment with anaesthetics the nuclei could be induced to divide amitotically, and that this amitotic origin in no way influenced the conditions of the subsequent development of the cells concerned, for these were capable of even proceeding as far as to form sexual cells, on the restoration of a normal environment. But in comparing amitosis and mitosis together, the advantage which the latter possesses, so far as can at present be stated, seems to lie in the accurate quantivalent distribution of all the structural elements concerned in the process between the two daughter nuclei. Whether this is the only advantage, or whether perhaps some mechanical or other factors are also involved, must be left to the future to decide.

In considering the general phenomena presented by karyokinesis, there are two sets of factors which, though closely interwoven in the process, may with advantage be kept as distinct as possible. For these changes involve the nucleus on the one hand and the cytoplasm on the other, and the degree of complexity which each of them may respectively assume is not necessarily invariable or correlative, either in different organisms or in different tissues of the same individual. A second, and not less important, consideration arises in connection with the fact that nuclear- and cell- (or cytoplasmic-) division are by no means invariably associated, and that although the cytoplasm never gives rise to a number of cells in excess of the number of nuclei present, its divisions in other respects may occur independently of that of the nuclei. This is seen in the cleavage of some animal eggs (*e.g.* mollusca), in the formation of endosperm in the seeds of angiosperms, in the development of the eggs of Fucus and of the spores of Mucor. In all these instances, the division of the nucleus precedes that of the cytoplasm, which is only subsequently partitioned.

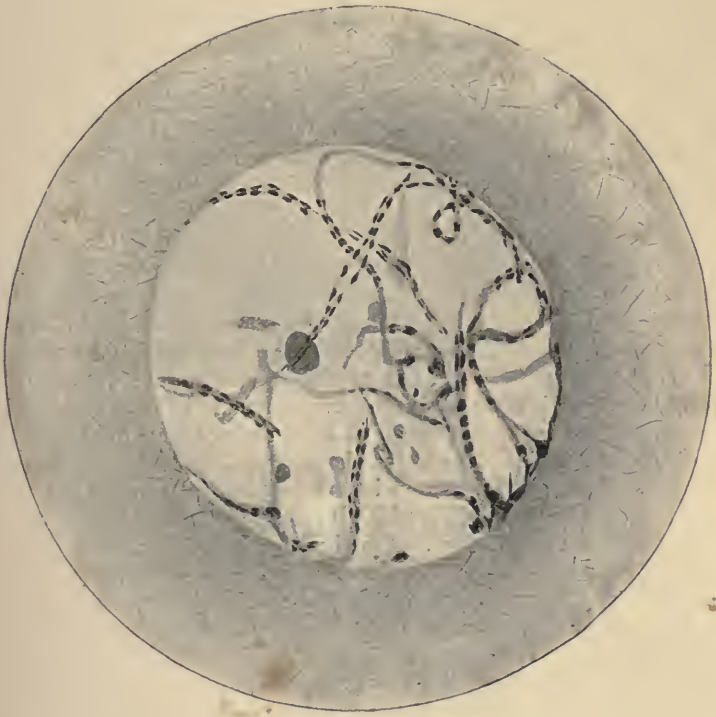

FIG. 8.

*Lilium martagon*, prophase of the first mitosis in the pollen-mother-cell, showing the longitudinal fission of the cromatin and linin.

The first indication of approaching karyokinesis in an ordinary somatic cell of the body of one of the higher plants or animals is usually visible in the nucleus. The chromatin granules become aggregated in lines, corresponding to a growing definiteness in the delimitation of the linin. Thus from the generally granular appearance, the character of a much convoluted and tangled chromatic skein is produced. The linin framework does not necessarily form a continuous thread. Often it is more or less broken, and it almost always shows cross-anastomoses (from which, however, in the later phases, the chromatin is commonly absent) with the neighbouring threads. This anastomosis is doubtless the expression of its segregation, due to contraction; the anastomoses themselves representing the original meshes by which the substance was formerly bound together into a coherent whole. Simultaneously the chromatin increases largely both in amount and in the intensity of its staining power—a fact which may be taken to indicate a chemical or physical change in its state. The linin thread-work that contains the chromatin is often not scattered irregularly through the nucleus, but is more or less polarised, as was clearly observed by Rabl, in such a way as to converge, often with considerable distinctness, towards one point on the nucleus. This point is occupied by the centrosomes when they are present. At first usually lying in pairs, and often in a mass of archoplasm, these bodies in the simpler cases now commence to diverge, and each is either accompanied by a portion of the original archoplasm, or else the latter is differentiated progressively and afresh as they move apart to take up diametrically opposite positions on the periphery of the nucleus. From them radiate outwards into the protoplasm the well-known astral figures which are characteristic structures in the cell at this period, and are commonly regarded as of archoplasmic origin.

Meantime within the nucleus the chromatic thread thickens and shortens. Some of its substance is probably derived, at least in many cases, from the nucleolus, which becomes vacuolated and often fragments about this stage. Finally, the thread breaks up into a number of segments which is constant for the somatic cells of the species. These segments are the Chromosomes (Waldeyer). At or immediately following this stage a fibrillar structure begins to appear within the nucleus, and as it increases the chromosomes are gradually driven to occupy an equatorial position (the equatorial plate stage) in the nucleus. What is precisely to be looked on as the origin of these fibrils (the so-called achromatic fibres which together form the achromatic spindle) is not certainly known. Some, with Strasburger, hold that they are exclusively of cytoplasmic (kinoplasmic) origin, growing inwards, as it were, from the polar centrospheres. Others again look on them as derived from nuclear substance, whilst a third view regards them as of mixed origin. Probably the last view is less open to objection than the other two. The fibrillar structures themselves are almost certainly the result of conditions of stress and strain in the viscous substances of which the cell is composed, and it would appear probable that any substance capable of assuming the fibrous character might be compelled to do so. And there is abundant evidence to show that such substances do exist in the nucleus, as they certainly do in the cytoplasm. For in the case of, *e.g.*, the micronuclei of infusoria, the whole spindle is entirely intra-nuclear, the cytoplasm apparently not furnishing, at least directly, any part of it.

With the congregation of the chromosomes to form the equatorial plate, the first stage or *Prophase* of division terminates.

The equatorial plate, or aster, stage is often one of relatively long duration; so much so that it may even happen that some of the signs of cytoplasmic activity may fall into temporary abeyance. For example, the astral radiations outwards from the centrosomes may cease to be visible at this stage (*e.g.* in Pellia), though they reappear later on. The nuclear wall commonly, though not always, disappears whilst the chromosomes are collecting at the equator, and the nucleolus or its fragments, if they have not previously disintegrated, now are no longer recognisable.

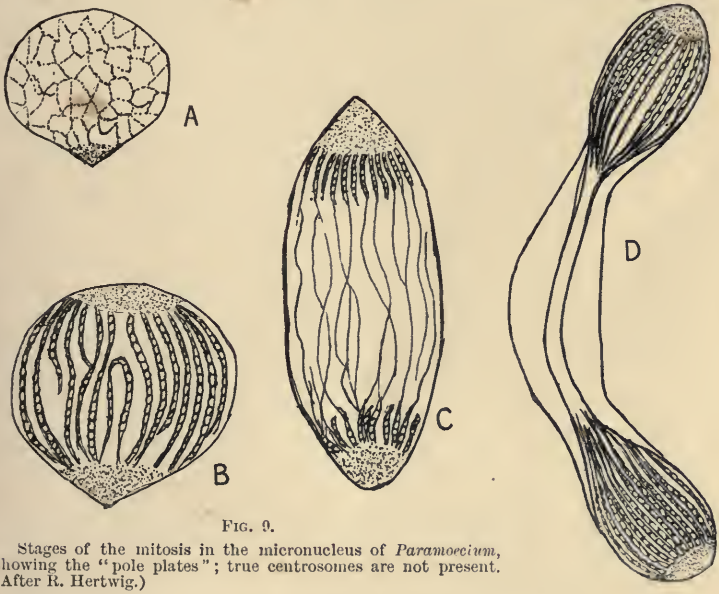

Fig. 9.
Stages of the mitosis in the micronucleus of *Paramoecium*, showing the "pole plates"; true centrosomes are not present. (After R. Hertwig.)

The individual chromosomes often, but by no means always, assume the shape of a V, with the apex turned centrally in the equatorial plane. Each one is supported by fibres of the achromatic spindle which run from the poles, and terminate on the chromosomes at the equator. The chromosomes next split longitudinally, and this partition forms the commencement of the stage known as the *Metaphase.* The two daughter halves rapidly diverge, being guided by the spindle fibres towards the poles. During their divergence

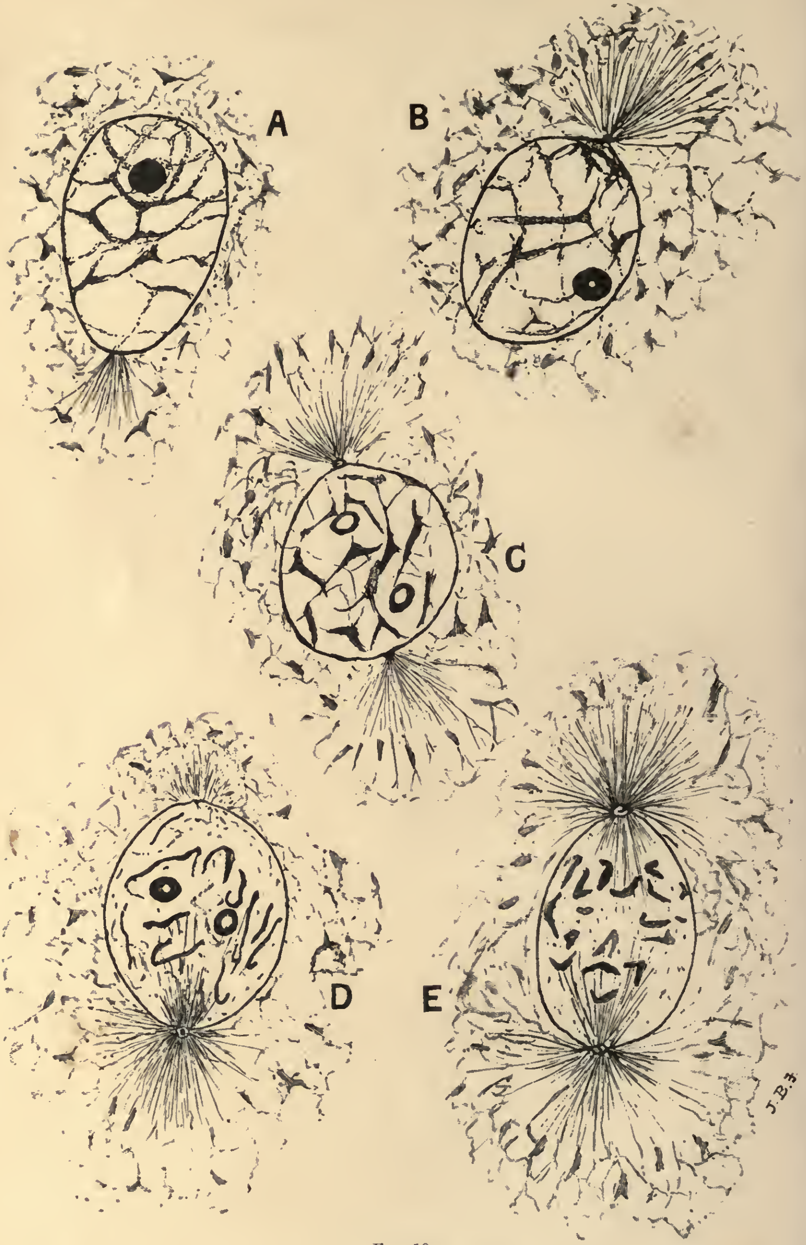

FIG. 10.

*Fucus vesiculosus*, stages in the first mitosis in the fertilised egg (oöspore). *A-D*, Prophase; *E*, commencement of the Metaphase.

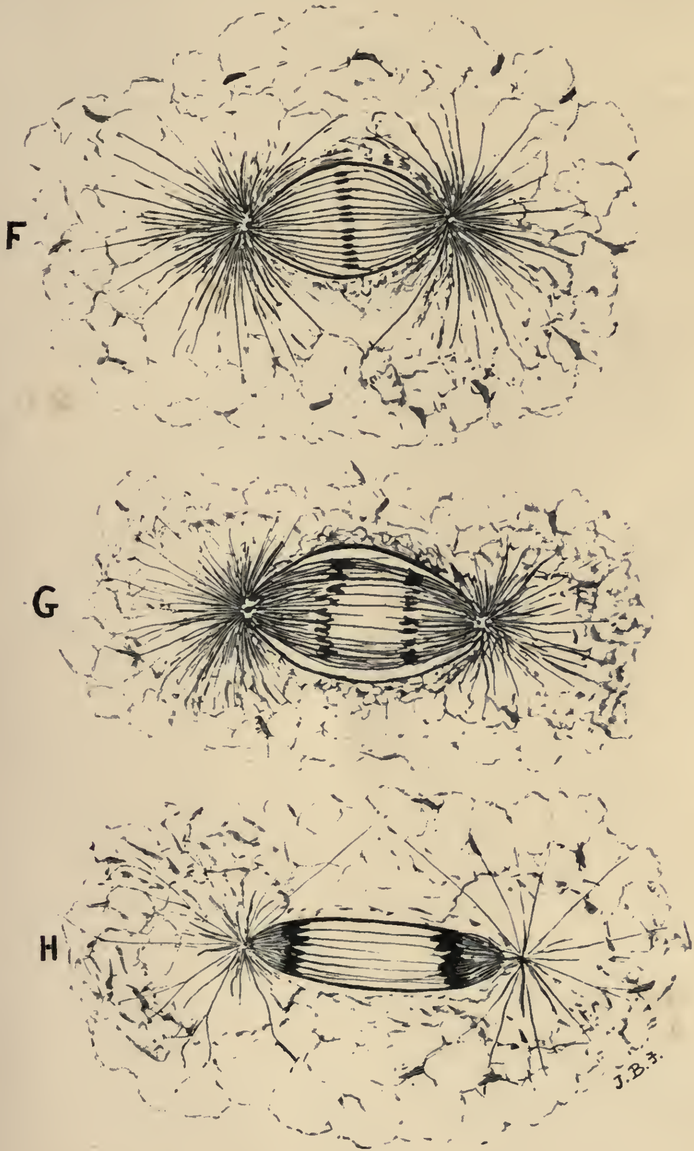

Fig. 10 (*continued*).

*Fucus vesiculosus*, stages in the first mitosis in the fertilised egg (oöspore). *F*, Metaphase; *G*, *H*, Anaphase.

fresh fibres are differentiated between the retreating groups of halved chromosomes, and form the interzonal fibres (Verbindungsfäden of the German writers). Whether these play any mechanical part in forcing the daughter chromosomes apart is uncertain, as is also the rôle assigned to the above-mentioned fibres that appear to direct the chromosomes towards the poles. Probably the latter are actively contractile, and there is some evidence to show that the interzonal fibres are in a state of stress. In some instances, *e.g.* in fertilised and segmenting eggs of Fucus, the arrangement of the elongated plastids in this region plainly indicate such a condition of stress or strain. But the achromatic apparatus varies considerably in the degree of its complexity, and it probably would be unsafe to attempt to assign constant functions to its constituent parts. So much, however, may be said, that the chromosomes appear to be

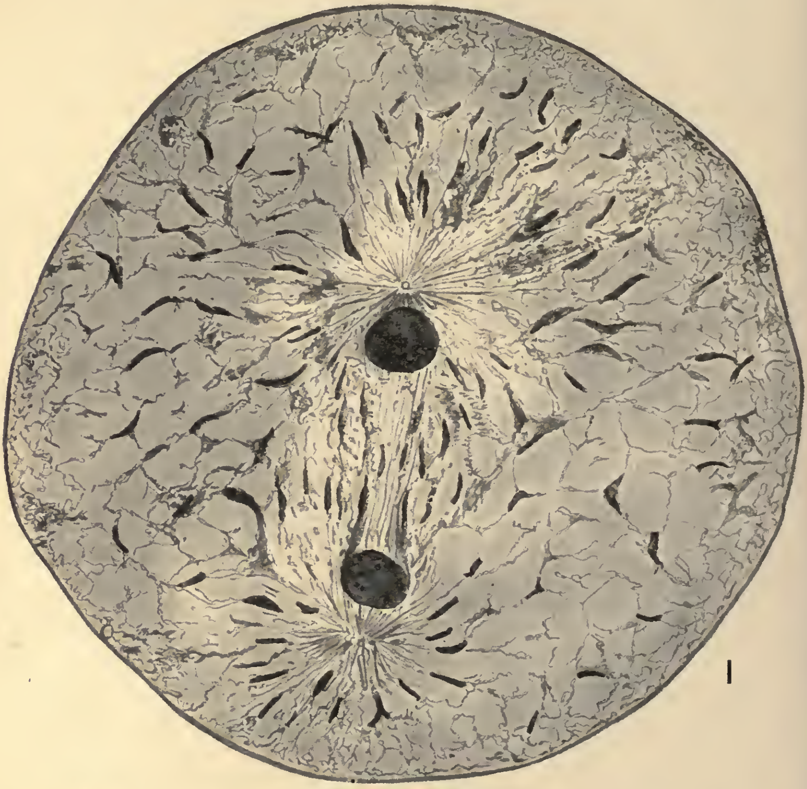

Fig. 10 (*continued*).
*Fucus vesiculosus*, stages in the first mitosis in the fertilised egg (oöspore). *I*, Telophase.
(*Phil. Trans. of the Royal Society.*)

*passively* moved to their respective poles, and to possess no power of automatic movement of their own.

With the arrival of the chromosomes at their respective poles the *Anaphase* stage supervenes. This consists practically in a series of regressive changes which leads to the formation of normal resting nuclei. The chromosomes lose their sharp outline and swell up; at the same time the nucleoli once more reappear. The chromatin, or as much of it as persists, is distributed through the swollen linin just as it originally existed in the parent nucleus, and finally a wall isolates the daughter nucleus from the surrounding cytoplasm. But the cytoplasm still bears traces of recent disturbances, and the period of gradual restoration of quiescence in it forms what is sometimes known as the *Telophase*.

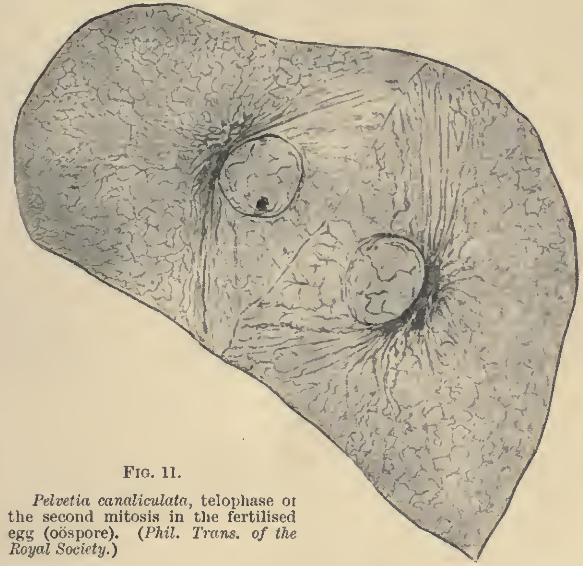

FIG. 11.

*Pelvetia canaliculata*, telophase of the second mitosis in the fertilised egg (oöspore). (*Phil. Trans. of the Royal Society.*)

The centrosome (when present) is often already doubled during the meta- or ana-phase, but the astral radiations frequently do not die away till much later. It is in the region of the interzonal fibres that events of the greatest interest are now proceeding. In animal tissues it very often happens that the two cells are constricted equatorially, and they may ultimately become delimited from each other, the remains of the interzonal fibres then remaining at this spot, where they may be long recognised as the *Intermediate Body.* In plants, owing to the existence of a cellulose skeleton, and the close adherence of the cytoplasm to its internal surface, such a constriction does not usually arise. Instead of this the fibres increase greatly in number, especially in the equatorial zone. In these fibres the primordium of the new cell-wall is laid down, in the first instance as a viscous film, but which later, by the deposition of fresh substances, becomes converted into the cellulose partition. Its mode of formation is interesting because reasons have been shown for supposing that some at least of the protoplasmic connections between adjacent cells are primarily effected by the permanence of such continuity through the membrane during its formation.

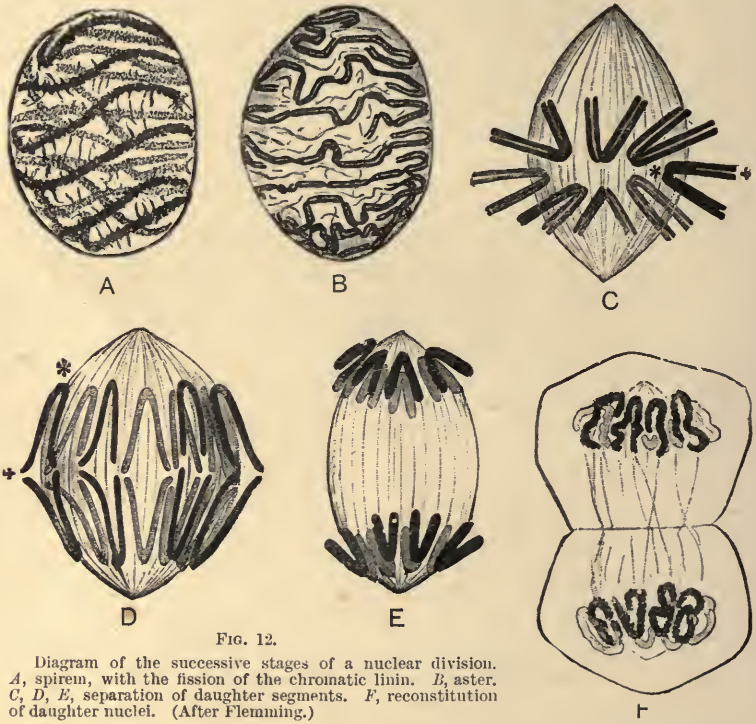

FIG. 12.

Diagram of the successive stages of a nuclear division. *A*, spirem, with the fission of the chromatic linin. *B*, aster. *C*, *D*, *E*, separation of daughter segments. *F*, reconstitution of daughter nuclei. (After Flemming.)

It may, however, happen that no membranes are formed in the interzonal fibres, such as will serve to delimit the daughter cells from each other. A complete series can be traced between the two extremes. Thus in the first division of the spore-mother-cell of Fegatella (Fig. 13), a cell plate is laid down, but not completed, and it is not until after the next nuclear division that this wall (which has shifted its position in the interval) becomes part of the final partitioning membranes. Again, in the endosperm of seeds, sometimes the embryosac is transversely divided after the first karyokinesis, but far more commonly a large number of nuclei are first formed. These then take up their final positions, and a *new set* of interzonal fibres are differentiated between them, and in the equatorial planes of these groups of fibres the cell-walls are laid down. And finally, in other cases the cytoplasm may divide into masses containing either single or several nuclei, and secrete membranes without the intervention of interzonal fibres at all.

It will have become evident from the foregoing account of the relation between the nucleus and the cytoplasm, that these two principal constituents of a cell retain to a considerable extent a separate individuality, at any rate in the higher forms. This separate nature only becomes obscured at periods of division, but even here, as has been seen, the essential boundaries are retained through all the changes connected with fission and redistribution. Thus it is legitimate to regard the cell nucleus as an entity which does not arise *de novo*. The nuclei of successive cell-generations are lineal descendants of an ancestral nucleus, just as the cells of the present day owe their being to the multiplication of antecedent parent cells.

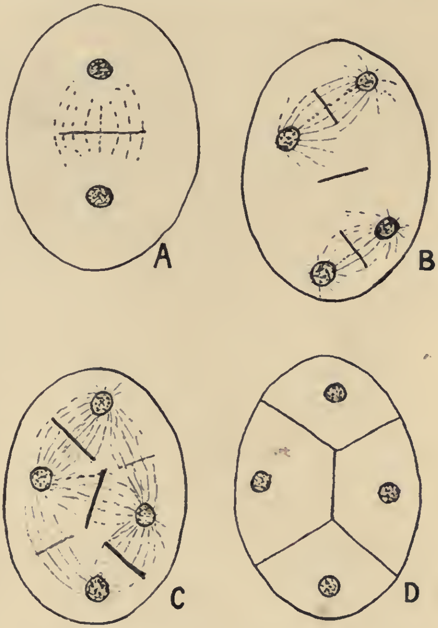

FIG. 13.

*Fegatella conica*, the division of the spore-mother-cell into four cells, showing the change in position of the first formed wall.

The nucleus, however, does not stand alone amongst the cell constituents as only arising by multiplication by fission of pre-existing structures of a similar character. In the plant-cell the various plastids originate in a similar manner, and there is no more evidence to show that they can be differentiated afresh from the general cytoplasm, than that the latter, by spontaneous generation, can arise *de novo* from its elemental constituents. The same is true for the curious coloured plastids known as Zoochlorella in animals, which possibly represent species of algae imprisoned in the cells of their animal hosts, or perchance, though less probably perhaps, they may be regarded as more akin to the chlorophyll corpuscles of the plant cell. The latter hypothesis would be difficult to sustain in the absence of a series of forms through which their evolution might be traced, whilst, on the other hand, the symbiotic relationship existing between fungi and algal cells in a lichen strongly supports the presumption that an analogous case is furnished by the Zoochlorella organism and its host.

### "*Reduction Divisions.*"

Few cytological discoveries have aroused more widespread interest than that of the periodical recurrence of the so-called "Reductiōn Divisions," which are intercalated at some point in the cell-generations intervening between two consecutive sexual unions. Each uniting gamete or sexual cell contains in its nucleus only half the number of the chromosomes that will be characteristic of the embryo resulting from their fusion, and will be retained throughout its cell-generations up to those which lead in their turn, more or less directly, to the production of spermatozoa and mature ova. This remarkable phenomenon has been observed in all the animals and plants which have been carefully studied, with the exception of the more lowly or primitive forms in which the nuclear history is but imperfectly understood.

The phenomenon in question was first made known by the investigations of Van Beneden in 1883 and 1887 on Ascaris. The choice of this animal was in some respects perhaps not very fortunate, since it does not exhibit the process in a very typical, but rather in an extreme, form, and thus a certain amount of misapprehension prevailed at one time respecting it. Since that period, however, very numerous animals and plants have been studied, with the result that the phenomenon is proved to be of very general occurrence, though differing considerably in detail in the various organisms.

At first, and perhaps naturally, the view was advanced that the reduced number was secured through the mere degeneration and consequent elimination of the superfluous chromosomes, but it gradually became clear that the evidence was entirely opposed to such a simple explanation, and that, on the contrary, the reduction was only arrived at after an exceedingly complex rearrangement of the nuclear constituents. It would, however, be going too far, as will subsequently appear, to deny that *any* nuclear substance is lost: all that can be said is that it is certain that no *chromosomes*, as such, are normally eliminated.

In attempting to trace the sequence of events, it must be borne in mind that the process is evidently one of the highest importance, seeing that it occurs alike in animals and in plants, and this importance is increased rather than lessened by the further recognition of the fact that the reduction may occur at morphologically diverse stages in the life-history of the various organisms —a fact which clearly emphasises its profound physiological significance. But although there is no lack of hypotheses to explain it, no one as yet has given a satisfactory theory which will embrace the whole range of the phenomena concerned.

In the higher organisms the process of reduction appears invariably to be closely bound up with two nuclear divisions which rapidly succeed each other, and are hence often spoken of as the Reduction Divisions. These differ in some important respects from those characteristic of other mitoses. They can only be considered in outline here, and after premising the existence of a not inconsiderable diversity as to the details of the process in different organisms. In animals the mitoses in question only occur in direct relation to the formation of the sexual cells or gametes, but in plants it is more usual to find a greater or less number of cell-generations follow on the Reduction Divisions before the actual gametes are formed. Thus it becomes obvious that the formation of sexual cells is not a necessarily immediate consequence of the change in the nucleus.

If the course of events be studied in an animal, it is seen that in the development of the spermatozoon and of the mature egg, a strictly comparable series of changes is passed through. Just as the spermatocyte gives rise, by two successive bipartitions, to four sperms, so the immature ovum, by means of two successive nuclear divisions, gives rise to four potentially fertilisable eggs, of which, however, three commonly degenerate and are known as the polar bodies.

The nucleus of the spermatocyte, just as does that of the immature egg (which may be distinguished from the ripe egg by the name of oocyte), goes through a somewhat prolonged period of growth before entering upon the critical mitoses. As these two divisions are marked by certain peculiarities from those of the other cell-generations, it is convenient to designate them by special names.

The first may be termed the Heterotype, the second the Homotype, mitosis, following the terminology introduced by Flemming. During a large part of the growth-period, leading directly to the heterotype division, the nucleus cannot be correctly described as resting, for the linin reticulum is plainly discernible, as also are the regularly arranged chromatin granules, which serve to render it distinct. In fact, this prolonged spireme is highly characteristic of the heterotype mitosis, as contrasted with those which have been previously gone through. It is during this stage that the fission of the chromatin granules occurs, as was first seen by Pfitzner in 1881. Each granule becomes drawn out into a dumb-bell-shaped body, and finally two rows of granules are seen to occupy the margins of the flattened linin riband.

This stage is often (Salamander, Helix, Lilium, etc.) followed by a more or less complete longitudinal fission and separation of the linin riband, each half now containing, at least at first, a single row of chromatin granules. It is perhaps not improbable that a similar process also occurs during the corresponding stage of somatic mitoses, but the shortness of its duration in the latter renders the process difficult to observe. At or about this period a remarkable contraction of the chromatic linin filament occurs, and commonly the nucleolus is included in the tangle. To this stage the name of Synapsis (Moore) has been given, and it seems to represent an important step in the process, and one which is confined to this first (heterotype) reduction division. After the synaptic condition is over, the linin, which has been getting richer in chromatin, is usually seen to be shortening, and at the same time thickening, but

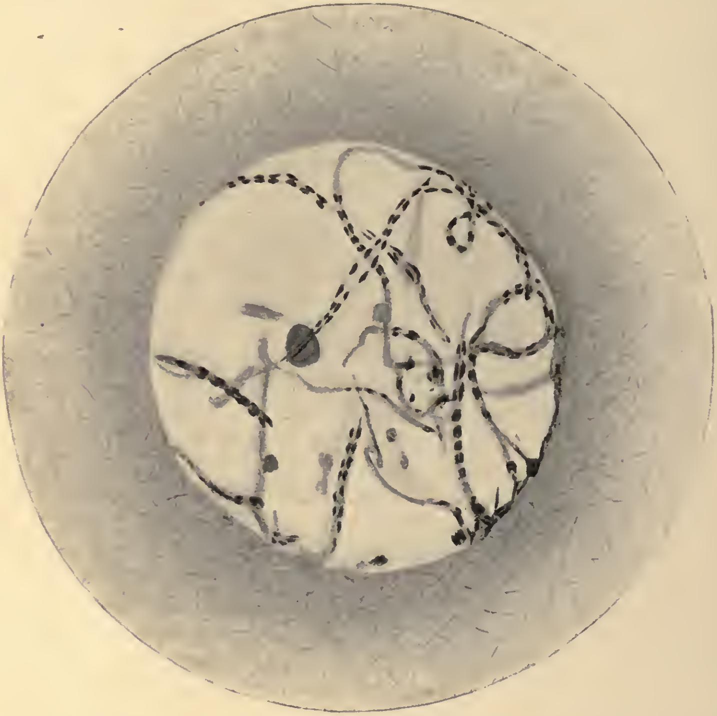

Fig. 14.

*Lilium martagon*, prophase of the first mitosis in the pollen-mother-cell, showing the longitudinal fission of the chromatin and linin.

it may happen that the subsequent events become much obscured, the filamentous arrangement of the linin and chromatin ceasing to be distinctly recognisable.

Up to this period there is, on the whole, a general agreement as to the nature and sequence of events, but the subsequent changes have been very diversely described and interpreted in the case of different organisms.

In the most favourable cases the parallel arrangements of the chromatin granules and of the split linin thread can be followed for some time during the shortening and thickening of the filaments. Brauer has described, for the spermatocytes of Ascaris, a *second* longitudinal fission in each chromatic filament, resulting in the production of four rows of chromatin granules from the single row originally present in the primitive thread. A similar event has been stated by some to occur in the corresponding division in the pollen-mother-cell of a lily. In the majority of instances, however, the chromatic linin is seen to contract and thicken, and all traces of the fission may become unrecognisable. Finally, the chromatin comes to be aggregated in definite parts of the band, the intervening portions being occupied by colourless linin. There are often, also, cross anastomoses of the same substance between neighbouring strands. The chromatic areas in question mark the position of the developing chromosomes (Fig. 15, *A*), which gradually become more definitely isolated from each other. And they are seen to be present in half the number characteristic of all the preceding nuclear divisions in the organism. Once more each chromatic band exhibits a split [1] along the whole or greater part of its length, and this marks the line along which, later on, the cleavage of the chromosomes in this (heterotype) mitosis will be effected. In many cases, as is especially well seen in amphibians (Fig. 15, *B*, *C*), the fission of the young chromosome is incomplete and the sides diverge, thus causing the whole to assume the form of a closed ring. In other instances, however, the fission is completed, and the two halves, lying in close juxtaposition, may exhibit a complex series of figures which demand much care in their elucidation.[2]

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[1] It is commonly assumed that this split represents the original longitudinal fission of the linin filament. It is not, however, proved beyond doubt that this is invariably the case.

[2] These appearances have, however, been differently explained by some investigators; thus some have seen in them evidence of an approximation of two *entire somatic chromosomes*, hence when the apparent halves separate to give rise to the chromatic part of the daughter nuclei, it would follow that what has really occurred is the distribution of half the original entire somatic chromosomes to the daughter nuclei. That is to say, the division might be regarded as qualitative as well as merely as quantitative. And it will be evident on reflection that the same result might be reached as the result of various analogous interpretations of the foregoing processes, especially when the difficulties of investigation that occur during the synaptic tangle are borne in mind

But the evolution of the chromosome does not always follow along these lines. In a number of instances, exemplified by many arthropods (*e.g.* Cyclops), after the early chromatic fission has been passed through, and the number of the future chromosomes has been marked out, these bodies, it is true, may form rings (Gryllotalpa) or parallel rods (Cyclops), but the chromatin, instead of being tolerably equally distributed throughout the length of the

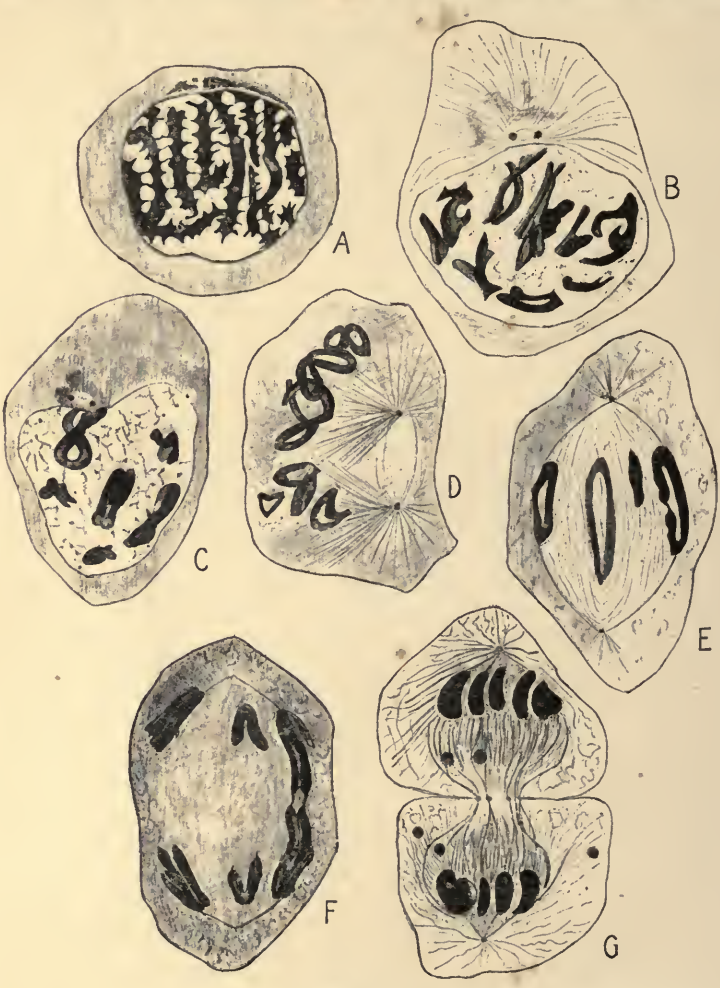

Fig. 15.

Salamander, Heterotype mitosis in the spermatocytes. (After Meves.) For explanation of the figures see the text.

longitudinal halves, becomes specially aggregated at two spots in each. Thus are formed the so-called *Tetrads*, to which much importance has been attached in the theoretical interpretation of the whole process of reduction. For it is thus seen that in the above cases the tetrad may be regarded as having originated first by a longitudinal fission of the chromosome rudiment, and then by a transversely isolated aggregation of chromatin in each half.

It may also happen that tetrads are formed in a manner less easy to follow out, as in Helix and in Arion, in which the separate filaments are difficult, if not impossible, to trace in the stages immediately preceding their formation; the chromatin thus appearing, so to speak, to travel to and become aggregated at definite areas, and to assume in a somewhat irregular manner the ring form of tetrad, similar to that occurring in Gryllotalpa, as described and figured by vom Rath.

Still another type of tetrad formation has been described by Brauer as occurring in the spermatogenesis of *Ascaris megalocephala* already alluded to above. The lining filament first contains a single row of chromatin granules, each of the latter divides crosswise into four, which lie in the same transverse plane, and hence the original filament now contains four rows of chromatin granules. As the process of shortening and thickening progresses, these become, so to speak, telescoped together, and the end view of each filament exhibits four chromatin masses corresponding to the four rows just described, and which thus appear as tetrads similar to those of Cyclops, although they would appear to have a very different origin. For whereas in the latter case the single units of the tetrad have arisen as the consequence of two longitudinal fissions of the original chromatin granules, in the case of Cyclops the same appearance is apparently produced partly by a longitudinal fission, and partly by a transverse delimiting of the original granules. In the first maturation division of the egg of the same animal, each chromosome is seen to be divided completely into four segments,

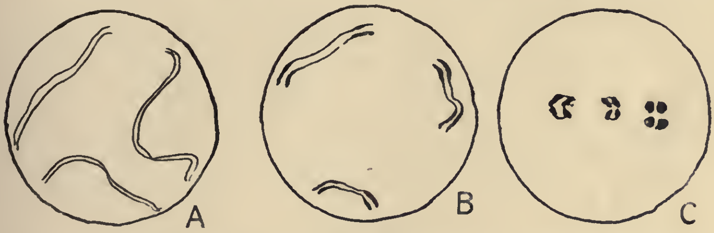

FIG. 16.

Diagram illustrating tetrad formation. *A*, the split thread (spirem) stage. *B*, later stage, showing aggregation of chromatin at each end of the split bivalent chromosomes. *C*, fully formed tetrads, of which the one to the right represents the most typical form.

though it is not certain as to whether the details of their development are similar to that of the spermatogenetic tetrads as described by Brauer.

Meanwhile, other changes have been proceeding, both within and without the nucleus. The nucleolus commonly can be seen to lose substance during the growth of the chromosomes, as is testified by its vacuolated appearance. Often it fragments into smaller particles during the prophases. But it has been definitely ascertained, in many cases, that some part of this body is cast out into the cytoplasm where it degenerates, and it is not improbable that this will prove to be of very general occurrence. The possible significance of this event ought not to be overlooked in view of its striking occurrence in the lower forms of life, for it is in them that the clue to the meaning of the complex changes observed in the higher animals and plants must probably be sought.

In the cytoplasm, also, remarkable changes connected with the centrosome and spindle mechanism have been proceeding. The latter reaches very different degrees of completeness in different organisms, and, as has been said on a previous page, even in the different cells of the same organism. In the simplest case the two centrosomes, when present, diverge and form a spindle not dissimilar from that already described for somatic nuclear division. In other instances (*e.g.* in Salamander) the two centrosomes diverge tangentially to the nucleus, and the spindle is formed between them, and, in the first place, without immediate reference to the nucleus. Later on, however, from the poles of the central spindle thus differentiated not only do the radiating fibrils reach into the protoplasm, and even to the periphery of the cell, but there are also others that extend to the nucleus and become attached to the chromosomes. The latter are thus, as it were, roped up and pulled on to the periphery of the first formed spindle (Fig. 15, *D*, *E*). Almost every gradation occurs between the extreme forms here sketched, and the matter seems to be essentially one of more or less complete division of labour between the constituent parts of the achromatic spindle regarded as a whole. In the Salamander, and those other cases in which it appears in a more or less complete form, the central spindle seems to function as a sort of support to keep the two poles apart, and to serve as a sort of railroad along which the daughter chromosomes can be pulled along by the contracting peripheral or mantle fibrils that attach them directly to the poles.

In the divisions of the higher plants, as has already been observed, no centrosomes have been identified with certainty, and the spindle at first starts into existence quite irregularly. It speedily, however, becomes for the most part bipolar, although not unfrequently isolated fragments of extruded nucleolar substance exert a very obvious influence on the direction of individual fibrils which may deviate towards and even terminate upon them.

When the chromosomes have reached the equator of the spindle they may still preserve the form of rings, tetrads, or more complex shapes, and the method of their fission which leads to the severance of the daughter chromosomes is seldom so clearly longitudinal as is the case in a somatic mitosis. The rings present the greatest difficulty, and there exists a considerable divergence of opinion as to whether their division really corresponds to a transverse or to a longitudinal fission of the whole chromosome. The answer practically turns on the conclusions arrived at as to the path of development followed by the chromosome during the earlier phases; *i.e.* whether the plane of separation really corresponds to that of the cleavage of the granules, or whether it may not be related to a totally different series of events, and marks the separation of originally bivalent chromosomes as is contended by some observers. In the latter case the complete identity of all the parent somatic chromosomes would be preserved in spite of its apparent loss through the fusion of them in pairs. The separation of the daughter chromosomes would be thus interpreted as not due to the fission of *one*, but as the segregation of each individual of a *pair* which had previously become temporarily united.

After the separation of the daughter chromosomes and the completion of the anaphase (Fig. 15, *G*) and telophase, the two nuclei which are thus formed commonly commence immediately to divide once more. Again the reduced number of chromosomes reappears, but the character of the process superficially resembles a somatic mitosis much more closely than the preceding heterotype division, and for this reason the name of homotype was given it by Flemming. In reality, however, there are many other points of difference, besides that of the reduced number of chromosomes. The first, and perhaps the chief, peculiarity lies in the fact that there is good reason for believing that the line of fission of the chromosomes is always predetermined during the prophases of the preceding, the heterotype divisions. This is strikingly seen in the case of Ascaris eggs, in which, during the first maturation division, two of the four rods that together represent one chromosome are distributed to the daughter nucleus as the equivalent of a single daughter chromosome, whilst at the second mitosis each chromosome emerges as a double (not quadruple) body, and at the metaphase the two constituent or collective parts separate from each other as the definitive chromosomes of the next (and final) nuclear generation. Essentially the same course of events obtains in cases of tetrads.

When these divide at the equatorial plate the resulting dyads thus formed retreat as the daughter chromosomes, and on the rapidly following homotype division the dyads again reappear in the early stages and divide at the equator, each half (monad) forming a daughter chromosome.

And an essentially similar condition obtains in at least many other more obscure instances. Thus in Salamander and in Tradescantia, during the dyaster condition of the anaphase of the heterotype, each daughter chromosome is seen to be longitudinally divided (Fig. 15, *F*). This almost certainly is the result of the reopening of a split formed during the prophase of the heterotype, but which has escaped recognition in many cases owing to the great difficulties which these earlier stages present in their investigation. And the fission, thus obvious in the dyaster of the heterotype, provides the daughter chromosomes for the next (homotype) mitosis.

It is thus seen that these two mitoses, the heterotype and the homotype, which in animals are the immediate forerunners of the differentiation of the sexual cells, are clearly distinguishable from the preceding ones in several important respects.

1. The appearance of the chromosomes in the reduced number, *i.e.* they are only half as numerous as in the rest of the nuclei.

2. The long duration of the prophase, and the complex changes and rearrangements, including, probably universally, a preparation for the distribution of daughter chromosomes not only for this but also for the succeeding division.

3. The remarkable forms assumed by the chromosomes upon the spindle.

4. The very general extrusion of nucleolar substance, in relatively large quantities, from the nucleus during the prophase. Although probably of importance, it would be as yet premature to speculate on the precise weight to be attached to this phenomenon, but it is suggestive when considered in relation to the course of events described for protozoa.

The accompanying figure may serve to render clearer the exact nature of the different views which have been held as to the nature of the processes which are passed through in the reduction divisions. The somatic cell (I. in the figure) is supposed to include two chromosomes, and below are represented, diagrammatically, the various alternative phases gone through during reduction, the corresponding stages being shown in any four figures on the same horizontal line. The series II. and III. represent the events which may be passed through on the assumption of the permanence of the chromosomes, whilst the series IV. and V. correspond to those in which such a permanence is denied. In the former case the two original chromosomes, A, B, remain temporarily united, and their two methods of possible separation are respectively shown. In IV. and V. no continuous identity is claimed for the chromosomes, and the two original ones are replaced by a single new one (C).

Considerable difference of opinion exists, then, as to the real nature, as well as the meaning of the events which are thus bound up with the two divisions under consideration. The indications

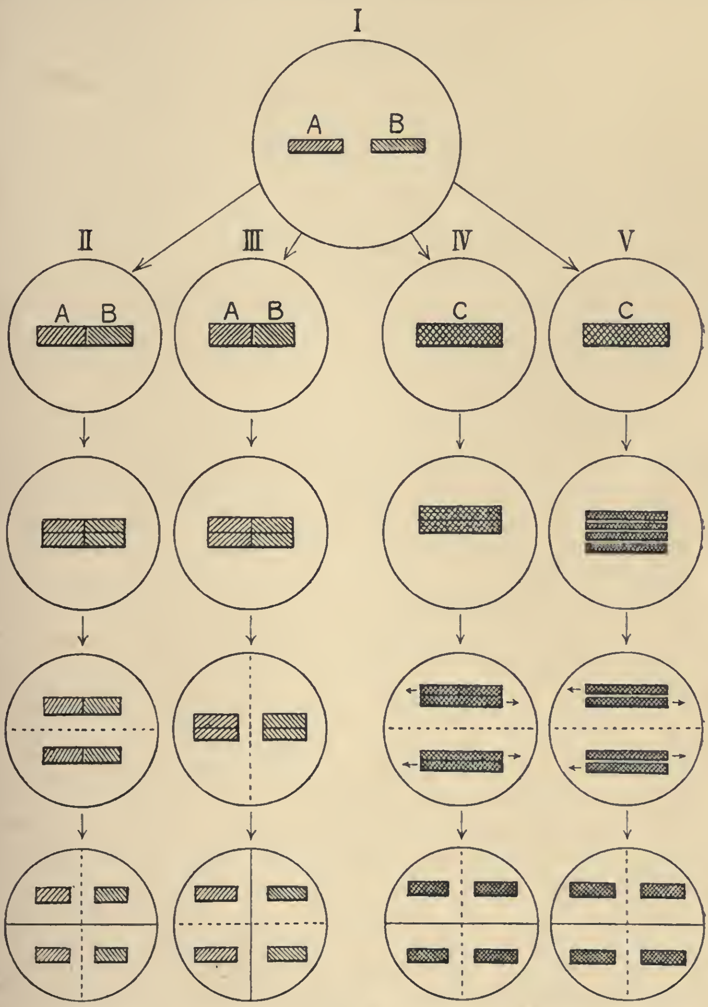

Fig. 17.

Diagrams of Heterotype and Homotype mitoses to illustrate the various possible ways of interpreting the chromosome distribution.

afforded by the constancy in number of the chromosomes through the cell-generations of an organism point to a morphological permanence, and it has been argued that the same chromosomes repeatedly are re-formed at each mitosis.

And since, during the reduction division, there is no evidence of the elimination or degeneration of any chromosomes, it is further urged that each of the apparent units appearing in the prophase of the heterotype division are really bivalent, and represent two chromosomes joined end to end, but otherwise behaving as one. Häcker, who has ably supported this view, believes, in common with many who share it with him, that the tetrad is to be thus explained. The longitudinal fission which divides the bivalent rudiment of the chromosome is succeeded by a more or less transverse separation or isolation of the chromatin, which marks the fourfold character of these chromosomes. Consequently each tetrad really represents not one but two chromosomes, and whilst the first (heterotype) division corresponds to the line of longitudinal cleavage, the second (homotype) separates and distributes actual *entire* chromosomes. Hence it is supposed that a real distribution of *entire* and diverse chromosomes occurs at the homotype mitosis, whilst the heterotype is essentially similar to a somatic division, and the reduction in number (due to the coherence in pairs) of the chromosomes is only an apparent one. If it could be universally proved to be true, such an explanation would account for many of the remarkable peculiarities which, as has been seen, characterise these divisions, besides affording a very strong support to the theoretical views as to the nature of the mechanism of inheritance advanced by Weismann. But the apparently well-established belief that in other cases the preparation for the two divisions is accomplished by means of two *longitudinal* divisions of the chromatic linin militates strongly against conceding the value of a general interpretation to the views just sketched in outline. And moreover the facts of amitosis as known to occur in some instances, also, though in a somewhat different way, tell against the permanence of the chromosomes, and consequently against the theories which have been founded on that hypothesis. On the whole, the facts at present before us rather tend to support the view of the brothers Hertwig; according to them the real significance of the process lies in that sudden quantitative reduction of the chromatin which is a necessary consequence of the rapid succession of the two mitoses in question.

It has already been pointed out that the reduction divisions are a common feature to both animals and plants. In the latter, however, there appears to exist a much greater latitude as to the point in the life-history at which they occur. In all the archegoniate series of cryptogams, which includes the mosses, hepaticae, and vascular cryptogams, as well as in all the flowering plants, the reduction divisions are not immediately connected, as they are in animals, with the formation of the sexual cells, but with the asexual spores from which the generation bearing the sexual organs arises. Thus, after the homotype (or second) division, an indeterminate number, which may be very considerable, of cell-generations intervenes between the division in question and the differentiation of the sexual cells. It is true that, as in some of the flowering plants (the embryosac development of the lily, for example), the divisions giving rise to the four spores may be omitted, but the characteristic features of the heterotype and homotype mitosis reappear, although thus postponed, in the first divisions of the nucleus of the embryosac (macrospore). This indeed is a fact of the utmost importance, as emphasising the physiological necessity of the process; just as it in all probability (from its community to animals and plants) preceded current morphological differentiation, so now if necessary it can override morphological limitations, or at any rate it is not bound up with them.

Amongst the lower plants the facts have been tolerably completely elucidated in the case of Fucus, an alga in which asexual spore-formation does not occur. The nuclei of the plant possess the double (somatic) number of chromosomes until the formation of the sexual organs. The oogonium gives rise to oospheres (typically eight, though some may degenerate) by these nuclear divisions. Of these, the first two are respectively heterotype and homotype, and follow on each other with great rapidity, the last mitosis not occurring till after an interval of rest.

In some of the desmids, and probably also in Spirogyra, there is evidence to show that the reduction divisions, on the other hand, occur not at the close, but at the beginning of the life-history, with the first segmentation of the fertilised oosphere. But in the majority of these lower organisms information of a precise character is still lacking on the matter. And until our knowledge of the corresponding processes in the lower animals and plants becomes much more complete than it is at present, we can scarcely expect to solve the problem as to the utility or the necessity of the complex events connected with the reduction divisions.

Although the higher animals and plants exhibit considerable diversity amongst themselves in the series of changes passed through by the nucleus in division, as well as in the relationships existing between the cytoplasm on the one hand and the cell-wall on the other, they nevertheless agree for the most part in the broader outlines. The points of similarity are, on the whole, more striking than are the differences, and the latter can often be referred without much difficulty to unimportant deviations from a common groundplan. But although this is the case, the actual meaning of the phenomena, as well as their phylogenetic origin (if there be one), can hardly be grasped or explained by a reference to these forms alone. It is in the study of the lowest forms of life that the key to the solution of cytological problems may be sought for with the greatest hope of success, for amidst the striking diversity exhibited in them an analysis of the processes may render it possible to distinguish between the essential and what is merely accessory, and may indicate the mode and directions in which the structures characterising the higher plants and animals have been elaborated. The essence of the type may perhaps be most clearly gathered from a consideration of the deviations from it. Nevertheless, one is confronted at the outset with difficulties. For although the nuclei of many protozoa are apparently extremely simple, yet in the details of their division they may exhibit considerable complexity, and this not by any means always in the direction followed by the nuclei of higher organisms. And conversely, nuclei are not seldom met with in these low organisms which surpass those of the metazoa and metaphyta in differentiation, whilst in mitosis they are commonly simpler.

The features which seem to be common to all nuclei are—(1) the existence of chromatin in some form or other; (2) a matrix in which the chromatin is imbedded, but which in the simplest cases may be indistinguishable from the ordinary cytoplasm. Furthermore, the fission of the chromatin is a common, perhaps invariable, antecedent to nuclear division, but it is often difficult to ascertain, and may possibly be really absent in some cases; for example, in many amitotic divisions.

The subsidiary structures, amongst which the centrosome stands pre-eminent, can only be rightly appraised when their origin has been traced in the lowest forms, in which various bodies which appear to possess functions analogous with those credited to centrosomes have often been distinguished.

As regards the occurrence of nuclei in the Protozoa and the simplest plants, the investigations of recent years have tended to reduce the number of those from which nuclei were formerly believed to be absent, and at the same time it has become evident that the structure in question may be present in very different degrees of completeness. Thus in Chromatium, and probably in bacteria generally, it is not possible to speak of the existence of a definite nuclear body, but granules which on good grounds have been identified with chromatin are to be distinguished in the protoplasmic framework of the cell. In the cyanophyceae also similar granules are visible, but are restricted to a definite specialised part of the cell-protoplasm, although the latter cannot be spoken of as a nucleus. In many of the forms which possess scattered chromatin granules there is visible in the cell a body which is obviously connected with the mechanism of chromatin distribution, for on cell-division the granules of the latter congregate around the central body, which sooner or later divides, each half carrying with it half the chromatin, in the form of attendant satellites, to each daughter cell. In some organisms, *e.g.* Tetramitus, the granules are distributed through the cell-protoplasm in the periods intervening between two fissions, and are only intimately associated with the central body at the time of cell-division; in others again, *e.g.* Chilomonas, they remain constantly grouped in the vicinity of the body to which reference has just been made. No structure has been certainly made out in it, but it has often been compared to, or identified with, the central body present in many of the more highly differentiated Protozoa, such as Euglena, and it has further been likened to the nucleolus and also to the centrosphere of those cells in which these structures have been found to occur. Indeed, it would seem that there is at least some justification for the latter comparison, inasmuch as it appears at least to discharge functions somewhat similar to those performed by the centrosome though in a very rudimentary degree.

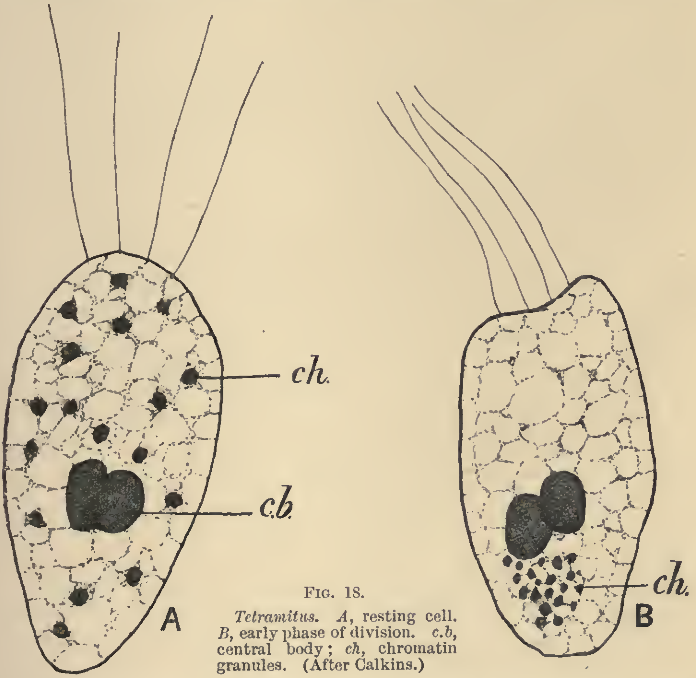

FIG. 18.

*Tetramitus*. *A*, resting cell. *B*, early phase of division. *c.b*, central body; *ch*, chromatin granules. (After Calkins.)

A distinct advance in differentiation is reached when the chromatic and other constituents of the nuclear apparatus are not only aggregated together, but are also delimited from the rest of the cytoplasm by a wall or membrane. The degree of individuality thus obtained provides a condition favourable to further specialisation, but it seems clear that at any rate the linin framework in which the chromatin is imbedded may be fairly traced back to a true cytoplasmic origin, however much it may have become modified or altered under more special conditions. The chromatin in these primitive nuclei is often aggregated into clumps as in Actinosphaerium, Noctiluca, Coccidium, etc., or even concentrated into one mass as in Actinophrys and Spirogyra. These masses have been termed nucleoli by some writers, but recent investigations tend to show that they really represent composite structures which contain other substances in addition to chromatin. In coccidia, for example, Schaudinn and others have shown that, although the chromosomes are derived from them, there exists over and above the chromatin a considerable mass of substance which is left behind after its exit, and much the same is seen in *Amoeba hyalina*. Possibly their analogues may be sought in certain of the so-called pseudo-nucleoli of the higher organisms, or in those occurring in the nuclei of Spirogyra, where it has been repeatedly asserted that the chromosomes originate from the nucleolus. As regards the origin generally of the chromosomes and of the peculiar features exhibited by them during mitosis, there seems but little doubt that they have arisen through stages like those seen in tetramitus and chilomonas, in which the distribution of isolated chromatin granules can be followed. The granules first become aggregated into definite tracts, and these form the primordia of the chromosomes themselves. The actual stages passed through are obscure, and even allied species exhibit considerable differences amongst themselves. Thus in the Amoeba, amitosis seems regularly to occur in *Amoeba brevipes* and *A. polypodia*, and also in *A. crystalligera*; but in *A. hyalina*, according to Dangeard, the chromatin separates from a central body and is differentiated to form chromosomes, whilst the remainder of the body gives rise to a rudimentary spindle which is entirely intra-nuclear. In *A. binucleata* the two nuclei divide simultaneously in a mitotic manner, and the same is true of the colonies of the amoeba-like myxomycetes. When a plasmodium is about to form spores, it may be found with nuclei showing typical karyokinetic figures, all the nuclei being in the same phase.

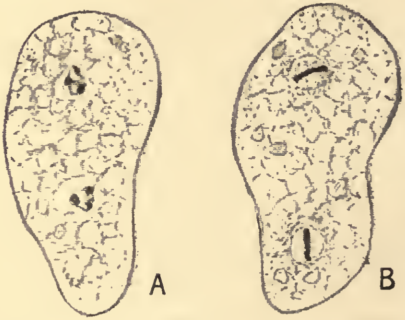

Fig. 19.

*Amoeba binucleata.* *A*, with resting nuclei. *B*, the two nuclei in the aster stage of mitosis. (After Dangeard.)

A remarkable dimorphism occurs in the nuclei of *Paramoeba eilhardi*, in which Schaudinn describes one of them as resembling a normal amoeban nucleus, whilst the other is much poorer in chromatin. During mitosis the two act as complements, the latter nucleus furnishing the spindle apparatus, whilst the former supplies the chromatin. Much speculation has been built on this case, which is assumed by some writers to indicate that the centrosome or centrosphere is equivalent, phylogenetically, to a nucleus. But it may be open to doubt whether the facts in Paramoeba have really been correctly interpreted, in the sense of regarding the spindle-forming structure as a genuine nucleus.

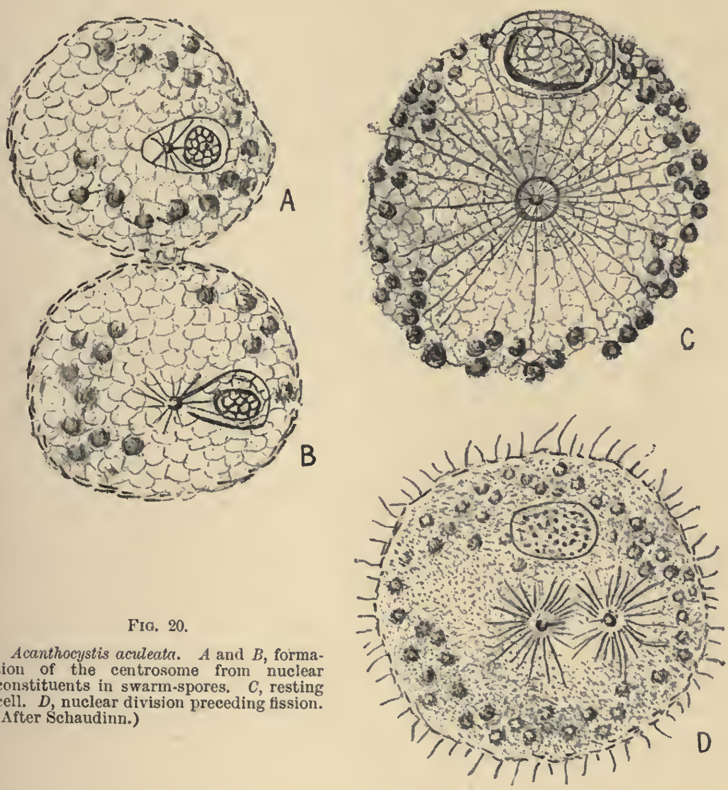

FIG. 20.

*Acanthocystis aculeata.* *A* and *B*, formation of the centrosome from nuclear constituents in swarm-spores. *C*, resting cell. *D*, nuclear division preceding fission. (After Schaudinn.)

Many cases are known in which bodies which represent centrosomes originate from the nucleus, as appears certainly to be the case in Actinosphaerium, and especially in Acanthocystis, as described by Schaudinn. In the latter animal the ordinary nuclear divisions are associated with the fission of a corpuscle or centrosome occupying a central position in the cell, the nucleus lying close to its side.

But in the numerous instances in which amitosis occurs (as in budding), the "centrosome" does not divide, and the nucleus of the freshly-budded cell possesses no such structure. Soon after the complete formation of the bud, however, a dense spot is formed within the nucleus, and is then extruded into the cytoplasm, where it continues to function as a centrosphere. The evidence, as drawn from a study of the lower organisms, seems to point strongly in favour of a nuclear origin for the centrosome apparatus in many cases, although the simplest examples cited on a previous page also indicate that, in others, such a structure might be coeval with, if indeed not actually antecedent to, the primary differentiation of a true nucleus.

In a considerable number of cases it seems at least clear that the body or the substance which stimulates and brings about the division of a nucleus is derived from the nucleus itself, even though it may migrate into the cytoplasm, where it may continue to exert, under appropriate conditions, that influence on the nucleus which culminates in division. Thus, in diatoms the centrosphere is found in the cytoplasm, just as it exists in many metazoon cells. The actual location of the centrosome does not necessarily, however, settle the question as to its real origin, and it may indeed assume an intra- or extra-nuclear position in closely allied forms; as, for example, in the two varieties of *Ascaris megalocephala*, being situated within the nucleus in the variety *univalens*, and outside it in the variety *bivalens*.

A remarkable side issue has been introduced into the controversy as to the phylogenetic origin of the centrosome by a consideration of the peculiar nuclear apparatus which is met with in most ciliata and suctoria. These organisms, with a few possible exceptions, possess a mega- and a micro-nucleus, the former presiding over the somatic life and divisions of the animal, the latter only becoming prominent during the phases of sexuality. Some writers have sought to derive, phylogenetically, the centrosome from the micronucleus, whilst they see in the meganucleus the representative of the metazoon nucleus. But quite apart from the fact that, as Schaudinn pointed out, centrosomes appear in the much simpler heliozoa, the fact that the micronucleus alone divides mitotically, whilst the meganucleus always does so by amitosis, seems a serious difficulty in accepting such an interpretation. Moreover, the macronucleus itself springs from the micronucleus after each sexual act, and only persists till the close of the sexual cycle, at which period it totally disintegrates, and thus suffers somatic extinction. It would certainly appear that at any rate it is useless to look to such a source for the origin of the centrosome, which really seems to rest on no better basis than a purely fanciful comparison.

A consideration of the maturation processes which obtain in the lower plants and in the protozoa when more fully understood will certainly shed light on the obscure phenomena exhibited by the higher forms, and may ultimately give the clue for correctly appreciating the general significance of the processes involved. It has already been remarked that the exact point in the life-history at which these remarkable divisions periodically recur is not identical for all organisms, whilst the universality of the process indicates clearly its great and fundamental importance. It has been urged by some that the chromosomes, which are by those writers postulated as permanent structures, become distributed between the daughter cells in such a manner that only half of the original number persist in each sexual cell. And in this way room is made for the new ones imported in either of the two conjugating gametes. Others again, like Oscar Hertwig, regard the quantitative reducing of the *chromatin* (as opposed to that of the *chromosomes*) as the fact of prime significance. In many of the lower forms, and notably in the coccidia, the evidence tells strongly for this view; for in them it is the definite fact that a large part of the mother nucleus is left unused when the gametes or gametocytes are produced, and thus there is a quantitative reduction of a very pronounced character. Again, in the same organisms the multiple division of the nucleus, taken together with the amitotic division of the nucleus of the zygote at segmentation, seem to tell equally against a mechanical necessity for similarity in the chromatic strands. It is not easy to believe in the permanent existence of specific chromosomes under such circumstances; but, on the other hand, there is no doubt that if the different chromatic granules do really represent slightly different structural characters, a qualitative reduction much in the sense assumed by him may actually take place. For there can scarcely exist any doubt but that, as the result of these processes, the surviving parts of the mother nucleus do not represent (especially after a multiple division) exact images of the original nucleus from which they have sprung. But it would also seem to be clear that whilst both a quantitative and a qualitative reduction have taken place, these can hardly be regarded as direct means of ensuring that an unvarying proportion of the original chromatin shall be distributed amongst the daughter nuclei. Whether the constant proportions observed in the higher forms is to be explained as the result of a more definite constancy in the chromosomes, together with the continuous existence of these structures in the hypothetically more specialised nuclei of the higher animals and plants, is a matter upon which it is as yet impossible to make any positive statement. It may, however, be confidently asserted, having regard to the extraordinary diversity which prevails in the details of nuclear transformations in these lower forms, many of which will be found described in the present volume, that amongst them, if anywhere, are to be sought the clues to the complex though less variable processes which characterise the higher animals and plants.

The phenomena of the sexual union of germ cells, and of their contained nuclei, for the most part are, as yet, hardly susceptible of detailed explanation, but there can be no doubt but that chemiotaxis is the proximate factor chiefly concerned. This is beautifully shown in the case of Halidrys, one of the Fucaceae, in which the large eggs attract numbers of sperms which seek to penetrate the egg. Immediately after an entrance has been effected by one of them, it is seen that the egg changes in important respects. It shrinks, and the supernumerary sperms instantly cease their endeavours to enter its substance. On the contrary, they swim rapidly away, and from the surface of the egg a substance is seen to be excreted which probably exerts the repellent influence in question. Indeed, so strong is its action that those sperms which have not quitted the surface of the eggs are rapidly paralysed and killed.

The remarkable paths followed by the male nucleus in the egg has been studied by many observers, and there can be but little doubt that here also a specific attraction of some sort effects the final union. As to the significance of the fusion, the evidence at present available points in no certain direction, nor can any of the hypotheses which have as yet been advanced to explain it be regarded as affording satisfactory solutions of the problem. It has been assumed that by its means a sort of rejuvenescence is effected. But this idea, which is not very clear in itself, fails to take the many subsidiary but still general recurring circumstances into consideration. Moreover, it is difficult to see why a similar explanation should not also cover those vegetative fusions common in endosperm cells and in certain fungal hyphae, but these have never been regarded as constituting sexual acts.

And indeed it would appear that the actual initiation of segmentation in an egg is not necessarily dependent on the fusion or even the presence of two nuclei. Boveri's observations on the fertilisation of enucleated fragments of eggs with sperms, and still more those of Loeb, who succeeded in causing the eggs of sea-urchins to segment parthenogenetically by treating them with magnesium chloride, indicate that the matter is of far greater complexity than a study of the normal occurrences would indicate. Again, Nathansohn caused parthenogenetic development of the oospheres of Marsilea to take place by keeping them at a sufficiently high temperature.

This last observation seems to be one of greater importance, for it suggests that a slight modification of the metabolic processes, in this case effected by the abnormal temperature, may suffice to set the machinery of segmentation in motion; that is, the actual mechanism is already present in the egg, and only an appropriate stimulus (not the importation of a missing half of the machinery) is required to set it in motion. Long ago Boveri suggested that the centrosome rather than the nucleus was the important body the introduction of which starts the process of segmentation, and it may well be that his suggestion, in a modified form perhaps, and without postulating an organisation of the specific excitatory substance in so definite a form as a centrosome, may contain a considerable element of truth.

Amongst the lower organisms, as Klebs and others have shown, the conditions favourable to the formation of sexual cells can be largely referred to nutritive sources, and this is only another way of saying that a definite stimulus—ultimately working on the living substance of the organism itself—is responsible for the sexual reaction.

But such a view of the matter leaves untouched the question of the secondary utility of sexuality as a means of ensuring variation. Indeed, this latter is perhaps best kept distinct from the primary causes and conditions which first made sex not only a possible but an inevitable incident in the life cycle of the greater part of the higher organisms.

Less obscure than its relations to the phenomenon of sex are those which exist between the nucleus and the life of the cell.

Gruber, Nussbaum, Verworn, and others have shown that in protoplasm which has been deprived of its nucleus the vital functions speedily become more or less deranged, and finally cease altogether. Enucleated fragments of a cell or organism fail to regenerate lost parts, and the apparent exceptions that have been met with constantly turned out, on further investigation, to be contaminated with nuclear influence. Enucleated fragments of an amoeba are unable to excrete the substance which normally enables these animals to cling to the substratum, and in other organisms, although food may be ingested, the protoplasm seems unable to digest and assimilate it. In plants Gerassimoff has shown that cells containing chlorophyll but destitute of a nucleus are usually unable to form starch, and are incapable of excreting a limiting membrane over their free surfaces.

On the other hand, allusion has already been made to the transformations the nucleus may undergo in connection with the secretory activity of glandular and other cells, and in this connection, no less than in that of regeneration, the nucleus may be affirmed to preside over the metabolism of the protoplasm.

The peculiar processes which are extruded by the nuclei of the nutritive cells surrounding the ovum (Ophryotrocha), and the curious simulation of the initial phases of mitosis met with in secretory cells, can hardly be dissociated from the special functions discharged by their nuclei.

Again, that frequent migration of the nucleus to the seat of special metabolic activity, so often illustrated in plants, affords additional indication of an exercise of the same influence. The developing of a lateral outgrowth on a plant hair, one-sided thickening of the cell-wall, the softening of the latter previous to its perforation—all these are commonly preceded by the arrival of the nucleus at the part of the cell about to be affected.

And the very facts of mitosis itself, with the profound chemical and physical changes which accompany it, suffice of themselves to prove that the nucleus contains substances which are capable of undergoing rapid and striking changes. And indeed it is perhaps not improbable that it is in that very lability characteristic of the constitution of the complex substances which together make up a nucleus that the supreme importance of this body to the cytoplasm, and through the latter to the organism as a whole, is to be attributed.

# THE PROTOZOA (*continued*)

## SECTION I.—THE FORAMINIFERA[1]

### CLASS FORAMINIFERA

Order 1. **Gromiidea.**
,, 2. **Astrorhizidea.**
,, 3. **Lituolidea.**
,, 4. **Miliolidea.**
,, 5. **Textularidea.**
,, 6. **Chilostomellidea.**
,, 7. **Lagenidea.**
,, 8. **Globigerinidea.**
,, 9. **Rotalidea.**
,, 10. **Nummulitidea.**

THE Foraminifera received their name before their nature was understood. The early anatomists, guided by the likeness of many of their tests to the nautiloid shells of the Cephalopod Mollusca, assigned them to this group, and many Foraminifera were included by Linnaeus and later writers in the genus *Nautilus.* D'Orbigny, in 1826, divided the "Cephalopoda," having chambered shells, into *Siphonifères*, with a more or less tubular siphon traversing the series of chambers; and *Foraminifères*, in which the chambers are in communication by foramina. The simple character of the organisms which secreted these shells was first recognised (1835) by Dujardin, who placed them with *Amoeba*, and allied fresh-water forms in the group *Rhizopoda.*

The limits of the group Foraminifera, as here understood, are identical with those of the Reticularia, as defined by Carpenter in his *Introduction to the Study of the Foraminifera* (8). It includes those *Protozoa the protoplasm of which secretes a test* (*or shell*), *and is protruded in fine thread-like pseudopodia, which branch freely and anastomose with one another, and present no obvious differentiation into ectoplasm and endoplasm.*

The great majority of the members of the group form a well-defined assemblage of organisms, clearly allied to one another, and distinct from any other division of the Protozoa; but we cannot at present draw with any certainty the limits between the simpler forms here included and some other simple members of the Protozoa.

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[1] By J. J. Lister, M.A., F.R.S., Fellow of St. John's College, Cambridge.

Each of the characters by which the group is defined loses in distinctness when followed into this borderland region. The shell, which attains great complexity in the higher forms, is membranous in many of the lower, and in *Lieberkühnia*, *Diplophrys*, and *Myxotheca* (Fig. 2) can hardly be said to exist. In *Hyalopus* the pseudopodia, though branching and pointed, do not anastomose with one another (Fig. 15), and in several of the fresh-water Gromiidae few anastomoses are found. The filiform nature which distinguishes the pseudopodia of the Foraminifera from the blunt-ended pseudopodia of the Lobosa is a better defining character; but in view of the close parallel which, as will be explained below, the life-history of *Trichosphaerium*, a member of the Lobosa, appears to present with that of many Foraminifera, its importance in a natural classification may be doubted.

A few of the simpler forms live in moor pools and other fresh waters, but the great majority are marine. Most of these are littoral in habitat; many extend their range to the floors of the deep oceans; while a small group, few in the number of species, but very abundant in individuals, lead a pelagic existence.

The *Protoplasm* presents a uniform character without any obvious separation into an outer and inner layer of different refracting power. It is finely granular throughout, and coarse granules are usually present in the protoplasm contained within the test.

The pseudopodia in some of the lower forms are long and root-like, and extend to great distances, giving off branches in their course, and to such forms Dujardin's name Rhizopoda is especially appropriate; but most members of the group are characterised by pseudopodia of a different nature (Fig. 1). They are for the most part very slender, and spread from the neighbourhood of the aperture or apertures of the shell in fan-like or sheaf-like groups. The outer surface of the shell is invested by a layer of protoplasm, and from this also groups of pseudopodia originate.

The pseudopodia frequently branch and anastomose in their course, and between the points of union of the reticulum which they form, they generally run straight, owing in part to the tension which they mutually exert on one another. Some of the radiating strands form broad bands, branching peripherally, but the majority are exceedingly slender, and the ultimate branches are of extreme tenuity. At the points of union broad expansions of protoplasm are often formed. The network of pseudopodia is in part projected free in the water, in part applied to surrounding objects, and serves at once for the prehension of food, as a peripheral sensory apparatus, and as a means of attachment and of locomotion.

When a strand of the reticulum is attentively examined, the granules contained in the protoplasm are seen to hurry along its

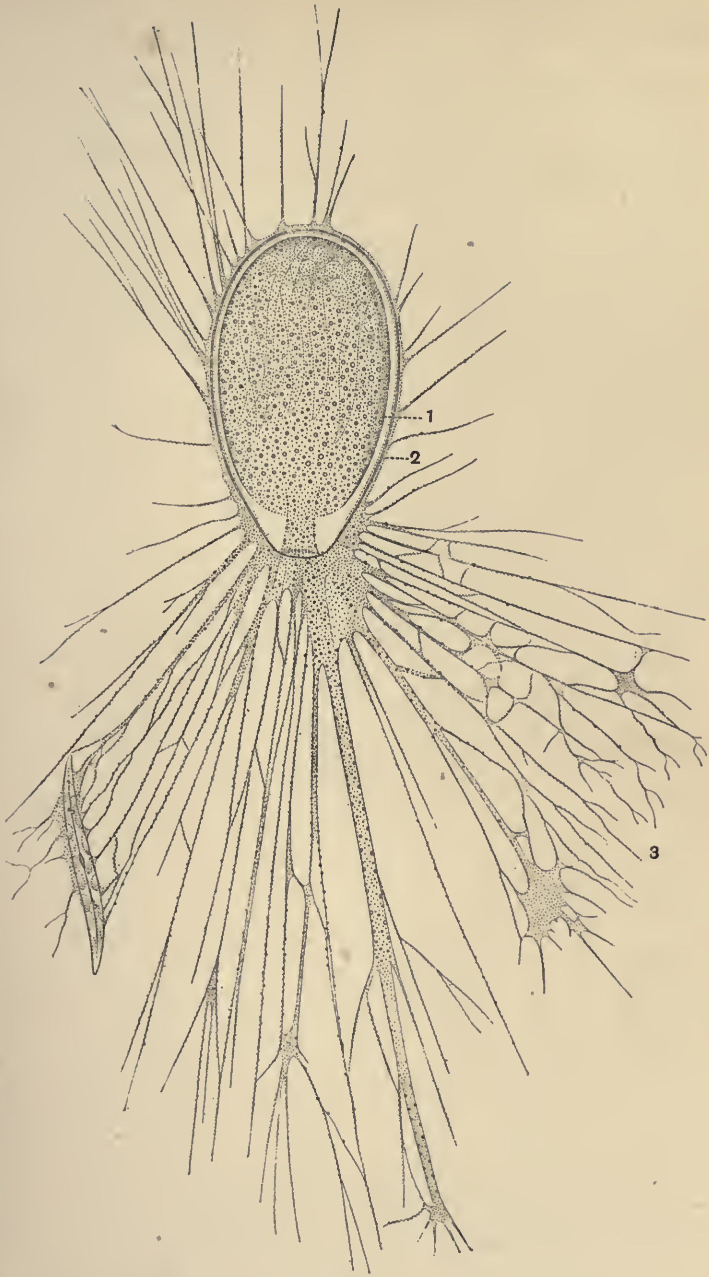

FIG. 1.

*Gromia oviformis*, Duj. 1, contour of protoplasm contained within the test; 2, protoplasm reflected over the test 3, extended pseudopodia. (From Shipley and MacBride, after Max Schultze.)

surface, as though borne by a stream, and two streams of granules flowing in opposite directions, centrifugal and centripetal, are to be seen on opposite sides of the same filament. Sometimes a mass of protoplasm forms a swelling on the surface, and is carried along for some distance before it thins out and merges in the substance of the filament.

The tip of a pseudopodium may be seen to be alternately extended and retracted according as the centrifugal or centripetal stream gains the ascendency. A mass more solid than the rest of the protoplasm may be seen to be carried to the tip, turn and pass back for some distance with the return current, then to be caught in the centrifugal stream, and again carried to the tip. One is reminded of a cork at the summit of a jet of water, under the contending forces of the upward flow of the jet and of gravity. But the cause of the streaming movement in the pseudopodia of the Foraminifera, like the ultimate cause of movement in all contractile tissues, is still beyond the limits of our knowledge.

The minute structure of the protoplasm has been carefully examined by Bütschli, who finds in the coarser pseudopodia, and in the membranous expansions between them, the alveolar structure which is present in so many protoplasmic structures. In the fine pseudopodia, however, this is absent, and they appear under the highest powers as homogeneous threads of extreme tenuity, with the small granules scattered along their surface. From the peculiar way in which, in the living pseudopodium, the granules course along the threads, sometimes leaving them for a moment to pass apparently through the open water, Bütschli is inclined to the view, suggested by Max Schultze, that an invisible hyaline layer may invest the visible threads of the Foraminifera in the same manner as the more visible hyaline ectosarc invests the axial endosarc of the pseudopodia of the Heliozoa.

In addition to this intrinsic streaming movement there is a movement of the reticulum as a whole. New pseudopodia shoot out from the central mass, others are shortened and retracted, and the whole system is in a condition of tension and constant movement, as becomes evident at once when an attempt is made to draw any part by camera lucida. When a strand of the reticulum gives way a momentary collapse of the neighbouring strands is seen, followed by the rapid lengthening of some strands and shortening of others, resulting in renewal of the tension.

The *food* of Foraminifera consists largely of diatoms and algae, either alive or in a state of decay. In some cases, however, it is of animal nature, for Rhumbler finds that the *Globigerinae* capture and digest the Copepods which abound at the sea surface, and that the pelagic *Pulvinulinae* contain the skeletons of Radiolaria as well as of diatoms, which have been taken as food (38, pp. 1 and 2).

Schaudinn also has witnessed the capture and digestion of a Copepod by *Myxotheca* (41, p. 25), and finds that *Patellina* and *Discorbina* feed on Copepod nauplii and Infusoria as well as on Diatoms (45, p. 182). The pseudopodia of *Gromia* and *Polystomella* have been seen to exercise a paralysing effect on Infusoria which come in contact with them (M. Schultze).

The pseudopodia are exceedingly viscid. When an object which serves as food is entangled it becomes surrounded by protoplasm, and if it is large the strands of the reticulum between it and the shell become thicker and more numerous, and the object is drawn inwards. Whether digestion may occur in the extended protoplasm or only after the food enters the shell is uncertain.

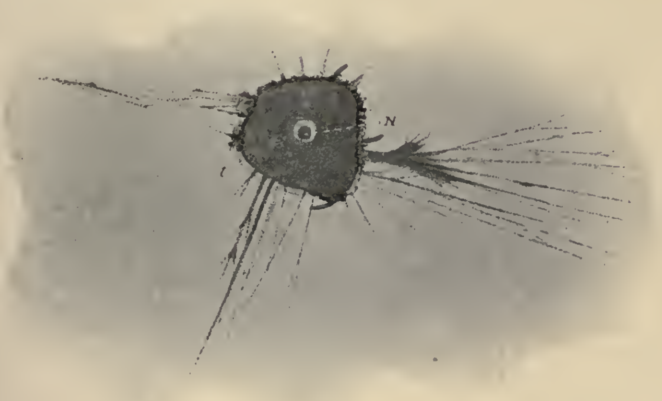

FIG. 2.

*Myxotheca arenilega*, Schaudinn. *N*, nucleus; *t*, the gelatinous test with embedded sand grains. (After Schaudinn, 41.)

*Contractile vacuoles* occur in some of the fresh-water forms (*Euglypha*, *Trinema*, *Cyphoderia*, *Microgromia*, and *Platoum*), but they have not been seen in any of the marine genera.

The granular bodies which are scattered through the protoplasm are of different kinds. Some are coloured, and confer a red, yellow, or brown colour on the protoplasm when seen in bulk. These are allied in composition to the colouring matter of diatoms (diatomin), and are probably derived directly from the food. Some are fatty; others, apparently proteid in nature, are stained by picrocarmine, and are probably formed in the ascending metabolism of the food. In *Orbitolites complanata* starch grains are abundant, but their formation is probably dependent on the presence of the parasitic algae (zooxanthellae) which abound in the protoplasm in this species. These algae also live in the pelagic *Globigerinae.*

The *nuclear* characters and modes of reproduction of the Foraminifera are considered below.

*The Structure of the Test.*—The *test* is found in its most rudimentary condition in *Myxotheca*, where it consists of a gelatinous layer, which may form the whole covering or may contain grains of sand. The shape follows the changing contour of the protoplasm, the pseudopodia break through at any point, and no definite and permanent orifice is formed. In *Hyalopus* (Fig. 15) the test is more resistent, and may have an oval form and a definite orifice; but here again the shape varies with that of the contained protoplasm, becoming arborescent when growing among the crowded stems of algae, and the number of orifices may be indefinitely increased (Schaudinn, 43). In most of the Gromiidea the test is chitinous and flexible; but it has a definite shape, and one or two permanent orifices.

Another type of test is found in some Gromiidea, and in all the Astrorhizidea and Lituolidea. The tests are here formed of foreign particles, such as fragments of sand, sponge-spicules, the shells of other Foraminifera, etc., fastened together by a cement, which may be firm or flexible, and consist of chitin or calcium carbonate or ferric oxide. In the Astrorhizidae the walls are thick and soft, consisting of mud, or of only slightly cemented sand (Fig. 17, *a*), while in other cases, as in *Saccammina* (Fig. 17, *b*), the particles are united into a rigid structure.

In some species of *Textularia*, *Quinqueloculina*, and other genera, though the tests are chiefly calcareous, a large proportion of foreign arenaceous material is contained in them.

A very remarkable feature of the tests of arenaceous Foraminifera is the evidence they appear to offer of a *selective power* exercised by certain species, in collecting materials. In some cases, no doubt, the nature of the test depends on the constituents of the sea bottom in which the animal lives, but in others certain elements alone are selected. Thus in the same dredgings may be found the tests of *Pilulina* and *Saccammina*, the former composed of a close felt of siliceous sponge-spicules, laid together to form a wall of uniform thickness; the latter of coarse grains of sand united by cement (Fig. 17, *b* and *c*). In both the test consists of a single spherical chamber, and the size attained is about the same in both. The cylindrical tests of *Bathysiphon filiformis*, Sars, are composed of a felt of sponge-spicules, covered externally by a layer of fine sand. The same sample of Pteropod ooze supplies representatives of species of the family Lituolidae, characterised by the coarseness of the sand grains of which the tests are composed; and of *Trochammina* distinguished by fine-grained tests.

The type of test found in *Euglypha* (Fig. 3) and its allies is very exceptional. It is formed of rounded or hexagonal plates, of siliceous or, in some cases, chitinous nature, which are secreted in the substance of the protoplasm in the neighbourhood of the nucleus. Passing to the surface, they are there built together into a regular test. With the exception of some forms of *Biloculina*, which have been found when living at great depths with a siliceous shell instead of the normal calcareous one, this is almost the only instance of the secretion by the Foraminifera of a siliceous skeleton—a fact which is all the more remarkable in consideration of the prevalence of siliceous skeletons among the Radiolaria and Heliozoa.

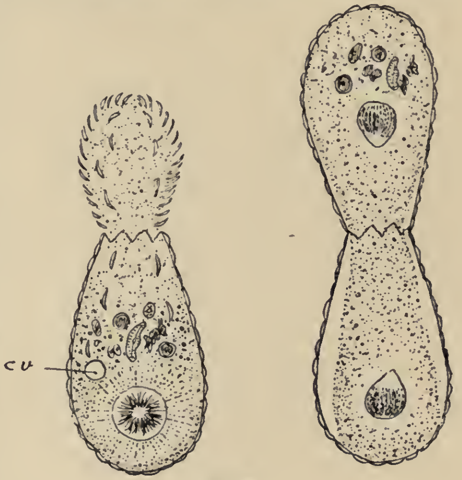

FIG. 3.

*Euglypha alveolata.* Two stages in the process of division. In one the nucleus is about to divide, and the plates which will form the new shell are seen in the protoplasm; in the other the division is nearly complete. *c.v*, contractile vacuole. (After Schewiakoff, 48.)

In most of the other orders of Foraminifera, though a chitinous element is present in the skeleton, it is only the basis in which carbonate of lime, together with a small proportion of carbonate of magnesium and traces of other salts, are deposited.[1]

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[1] The following analyses are given by Brady (3, pp. xvii. and xxi.) of the tests of two species—one porcellanous, belonging to the Miliolidea; the other perforate (see footnote, p. 54), a member of the Nummulitidea :—

*Orbitolites complanata*, var. *laciniata*.

| | |
|---|---|
| Silica | 0·14 |
| Carbonate of lime | 88·74 |
| Carbonate of magnesia | 9·55 |
| Alumina with phosphate of lime and magnesia | occasional traces |
| Alumina and ferric oxide | |
| | 98·43 |

*Amphistegina lessonii.*

| | |
|---|---|
| Silica | 0·30 |
| Carbonate of lime with a little organic matter | 92·85 |
| Carbonate of magnesia | 4·90 |
| Alumina with phosphates of lime and magnesia | 1·95 |
| Ferric oxide | trace |
| | 100·00 |

Sollas has examined the specific gravity of the shells of perforate and imperforate species of Foraminifera (66, p. 374), and finds that in perforate forms it varies from 2·626 to 2·674. In examples of *Miliola*, *Peneroplis*, and *Orbiculina* it varies from 2·7 to

In these the tests are rigid structures, and communicate with the exterior either by one or more large apertures exclusively, as in the majority of the Miliolidea, or by a multitude of small pores in their walls in addition to the large apertures.[1] In some genera of the Miliolidea the shells have a polished white appearance resembling porcelain when seen by reflected light, and a yellowish brown horn colour when seen by transmitted light; in the perforate forms the tests are more transparent, and are in many cases as clear as glass. On this account the forms with perforate calcareous tests are often known as the *vitreous* or *hyaline* Foraminifera.

In the perforate forms the pores passing out from the chambers have, on the whole, a direction perpendicular to the walls, and transmit pseudopodia. In some cases the pores are large and comparatively few, in others they are fine and very numerous.

*The Growth of the Test.*—In forms such as *Myxotheca* and *Gromia* the growth of the protoplasmic body is accommodated by the simple expansion of the soft and membranous test. Among the arenaceous forms, the feebly cemented, star-shaped tests of *Astrorhiza* (Fig. 17, *a*) increase in size in part by the extension of the test along the protoplasmic trunks forming the rays of the star, but in part, doubtless, by the expansion of the central body. In the case of *Saccammina* (Fig. 17, *b*), however, and other forms with rigid single-

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2·722. The specific gravity of calcite is 2·72, and that of aragonite 2·97. He concluded that the calcareous constituent of the perforate tests is calcite, and that of the imperforate tests either aragonite or calcite together with some other and heavier substance. Cornish and Kendall (12) had previously indicated the conclusion, though without positively stating it, that the porcellanous Foraminifera were composed of aragonite—on the grounds of their opacity, and their appearance in or absence from beds coincidently with Lamellibranch and other fossils which are composed of aragonite. Chapman (11, p. 39) also has recently stated that the tests of the *Miliolidea* are of aragonite, or rather (following Miss Kelly, *Mineralogical Mag.* vol. xii. (1900), p. 363) conchite.

I am inclined to doubt this conclusion. It appears that the presence of the magnesium carbonate (specific gravity 3·056), which Brady's analysis shows is a larger constituent of the imperforate tests than of the perforate, may cause the higher specific gravity found in the former by Sollas. Moreover, Meigen (22) has recently described a chemical colour test by which calcite may be distinguished from aragonite, or from the constituent which Miss Kelly has named conchite. Tried by this test, I find that *Miliolina* and *Orbiculina* and *Orbitolites* do not give the colour reaction characteristic of aragonite, but agree with structures composed of calcite. I am indebted to Mr. A. Hutchinson for calling my attention to Meigen's paper.

[1] In the systems of classification prepared by Reuss (1861) and by Carpenter and his colleagues (1862) the Foraminifera were divided into the two groups, the Imperforata and the Perforata. In the latter classification the group Imperforata includes the *Gromida*, *Lituolida*, and *Miliolida;* the Perforata the *Lagenida*, *Globigerinida*, and *Nummulitida* (*i.e.* families 5-10 of Brady's classification, which is followed in this article). The progress of deep-sea investigation since this date has revealed the existence of the Astrorhizidea, some of which have perforate and others imperforate tests. Moreover, even in the Miliolidea the first formed chambers may be perforate in the genus *Peneroplis* (Rhumbler), and in *Orbiculina* and *Orbitolites*, as shown in this article. It thus becomes evident that the presence or absence of perforations in the shell, though perfectly characteristic of many of the orders, cannot be taken as the basis for the subdivision of the whole group.

chambered tests, the way in which the growth of the protoplasm is accommodated is less obvious.

It is probable, however, that here also the shell, though at any particular moment rigid, is slowly moulded and expanded under the influence of the protoplasm. The small tests hitherto classified as *Psammosphaera fusca*, but regarded by Rhumbler (33) as the young of *Saccammina sphaerica*, with which he finds them to be connected by all intermediate forms, are built up of fragments of sand placed together irregularly, so that the contour of the young test is rough and uneven. In the full-grown *Saccammina* test the fragments are placed, as in a well-constructed stone wall, to form an even contour. If, as these facts imply, a change in position of the constituents has occurred during growth, there is no difficulty in accepting the conclusion at which Rhumbler arrives, that it has also undergone expansion as a whole. The alternate hypothesis, that in the course of growth to its full size (3·5 mm.) the protoplasm periodically discards its old shell and builds a new one, appears improbable, and the student of the growth of bone will find no *a priori* difficulty in admitting that a rigid structure may be the seat of profound interstitial changes of substance.

The growth of the tests of the cylindrical forms of the Astrorhizidea is effected by extension in a linear direction, fresh arenaceous material being incorporated at their ends. They form simple or branched (many *Hyperamminae*, *Rhizammina*), but usually unsegmented tubes. In *Hyperammina subnodosa* (Fig. 17, *d*) the tubes are constricted at irregular intervals, and thus present a transitional condition of structure to the definitely segmented, chambered shells of the great majority of Foraminifera. In the latter, while the growth of the protoplasm as the result of the assimilation of food is continuous, the growth of the shell is not continuous but periodic. When a new chamber is to be formed, a mass of protoplasm is protruded from the mouth of the shell, and at the surface of this the new wall is formed, by secretion in the case of calcareous shells, by cementing together of foreign elements in the arenaceous forms. In some genera the secretion of shell substance takes place only on the free surface of the protoplasm, but in others it occurs also where the protoplasm rests against the previously formed test. In such cases the septa dividing the chambers are double, and the new chamber is complete on all sides with the exception of the aperture or apertures left for communication with the exterior, or with its successor, when a new chamber shall be added. In either case the result of this periodic shell formation is the building up of a segmented test, the segments of which, the chambers, are sharply marked off from one another.

Max Schultze found that in the formation of a new chamber by *Polystomella*, the deposit of calcareous salts began before the chamber had assumed its final form. The small pocket-like "retral processes," which are characteristic of this genus (see Fig. 7), were not formed until some time after a continuous wall had been secreted, so that a partial absorption and re-deposition of the lime salts must here occur (64, p. 30).

*Structure and Mode of Growth of the Shell Wall.*—After their first formation by secretion at the surface of a mass of protoplasm, the walls increase in thickness by the addition of shell material to the outer surface. The anterior wall of each chamber is soon covered by the addition of a new chamber in front of it, and it then forms the whole, or half (as the septa in the species concerned may be single or double), of the septum dividing the chambers from one another. On the septa of the perforate forms the pores may be limited to the peripheral parts or absent altogether.

The thickness attained by the septa is not great, but the part of the wall turned to the outer world continues to grow, and may attain considerable thickness.

The thickening results from the addition of successive layers of material on the outer surface, and thus a laminated structure is produced; but though laminated tangentially, the shell is built up, where it is perforated, of hexagonal prisms disposed radially to the surface, and each traversed by a pore transmitting a pseudopodium.

It appears that this result may be explained as follows. The shell material is deposited by the protoplasm traversing each of the pores which perforate the wall, on the area about its orifice. It would appear that at the limits between the areas influenced by neighbouring pseudopodia there is some slight difference in the character of the material secreted, and the result is that the deposit is not quite uniform, but marked out into small hexagonal areas, with a pore at the centre of each. If this is the case, the prismatic structure results from the observance of the same limits in successive layers throughout the thickness of the shell.

In the more complicated perforate Foraminifera a system of sinuses or canals is present, the main channels of which run in the substance of the shell, and are distinct from the cavities of the chambers, though communicating freely with them by branches. This is known as the *canal system*. It is, of course, wholly distinct from the radial pores leading direct from the chambers to the exterior. The details of its distribution in *Polystomella* are given below (cp. Fig. 9). It will be seen that in this form two main "spiral canals" run on either side of the test, parallel with the series of chambers, and give off branches, some of which run in the thickness of the septa between the chambers, while others pass direct to the exterior in the axial regions of the test. About the ultimate branches of the canal system a deposit of shell substance is laid down, which may be called the *canalicular skeleton*. In the test of *Polystomella* this skeleton is mainly limited to the axial regions, but in other genera it forms extensive deposits in the interior of the septa, and on the surface of the test. It attains a great development in *Calcarina*.[1]

Where the canalicular skeleton comes in contact with that of the chamber walls, the two merge insensibly into one another; the only distinction between them is that one is penetrated by the branches of the canal system, the other by radiating pores leading direct from the chambers of the test.

Some confusion has arisen in the use of the terms intermediate or supplemental skeleton, and proper chamber wall. In the *Introduction to the Study of the Foraminifera* (p. 50) Carpenter says that the "intermediate or supplemental skeleton" is "formed by secondary or exogenous deposit"; and further, that wherever developed to any considerable extent, "it is traversed by the canal system." The statement that the supplemental skeleton is formed by a secondary or exogenous deposit appears unfortunate, for the walls of the chambers of all the perforate calcareous forms are at first exceedingly thin, and they increase in thickness by the deposition of shell substance on their outer surface, so that the greater part of the shell in all may be said to be secondary and exogenous. The part of the shell first formed is in most, if not all, cases quite indistinguishable from that which is added later.

The second character of the supplemental skeleton given by Carpenter, that it is traversed by the canal system, does, however, touch on a real distinction.

Bütschli (6, pp. 26-27) calls attention to the fact that a difference between a primary shell layer (Carpenter's "proper wall") and a *secondary mass* is often indistinguishable; but he proposes to use the latter term for the outer layer of the shell, whether unperforated, perforated by radial pores, or by branches of the canal system.

It appears to be more advantageous to distinguish the skeleton developed in relation with the canal system from that of the chamber wall, and as confusion is attached to the name supplemental skeleton, the term canalicular skeleton is used in this article for the former.

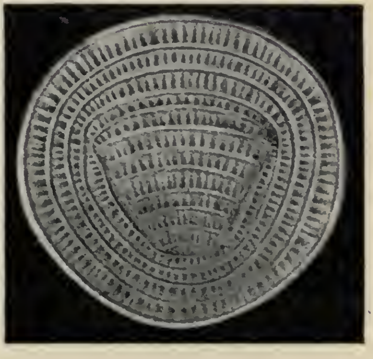

FIG. 4.

Specimen of *Orbitolites tenuissima* in which a fragment of a test has given rise to a new disc. (From Carpenter, 9, Plate I. Fig. 7.)

*Repair.*—The power of repairing injuries is very great, and indeed a fragment may, in some cases, give rise to a new individual. This is well seen in the specimen of *Orbitolites tenuissima* shown in Fig. 4, in which it is interesting to note that the centre of symmetry of the growth which occurred after the injury is entirely different from the original one.

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[1] Cp. Carpenter, 8, p. 216.

Verworn (67, p. 455) finds that when a specimen of *Polystomella crispa* (his observations were doubtless made on megalospheric forms, see below) is broken into fragments, several of the larger pieces remain alive and extend pseudopodia, but new shell is secreted over the broken surfaces by only one, and this is found on examination to be the fragment in which the nucleus is contained.

*The Form of the Test.*—The principal forms of test met with among the Foraminifera will be considered later. We shall see that in some genera a particular mode of growth, in relation to some simple symmetrical plan, whether rectilinear, plano-spiral, helicoid, or annular, is observed with perfect regularity, while in others a symmetrical plan is only loosely followed. Many species are adherent to other objects, and in them the chambers may be "heaped" together irregularly, forming what are known as the "acervuline" tests.[1] Some of the adherent forms take on an arborescent shape.

*Multiform Tests.*—A remarkable phenomenon is presented by many genera, and that is that the plan on which the chambers are arranged in the growth of the test changes in the course of growth. In such tests the chambers which succeed the central one are arranged on a particular plan, whether plano-spiral, helicoid, or some other, and after growth has progressed on this plan for some time a change occurs, and a new plan of growth is with greater or less abruptness adopted (Figs. 24, 39, 40, 44, etc.). In some cases the plan of growth may be changed more than once before the test is completed. Thus two or more types of arrangement of the chambers are, in these genera, presented by the same test at different stages of its growth. The genus *Spiroplecta* is an example in which the chambers are at first uniserial and arranged in a plano-spiral, and later biserial and in a rectilinear series (Fig. 44, A and B). To tests exhibiting such different modes of growth the terms dimorphic, trimorphic, and polymorphic (according to the number of forms of growth present) were originally applied, and the phenomenon of their occurrence was spoken of as dimorphism, trimorphism, or polymorphism. But it has since been discovered that two kinds of individuals occur in the life-cycle of many Foraminifera, and for this, which is, of course, an entirely distinct phenomenon, the term dimorphism has, in accordance with customary biological usage, been adopted. It has thus become necessary to find other terms to characterise tests displaying two or more modes of growth, and the adjectives *biformed* and *triformed* may, as proposed by Rhumbler (36, p. 63), be conveniently used for this purpose. In what follows I have used the term *multiform* to cover any departure from the uniform condition of growth.

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[1] *Acervus*, a heap.

It is shown below that while in some genera both forms of individual which are found in one species are alike bi- or tri-formed, in others the phenomenon is exhibited by only one form (the microspheric), or exhibited by it to a greater degree.

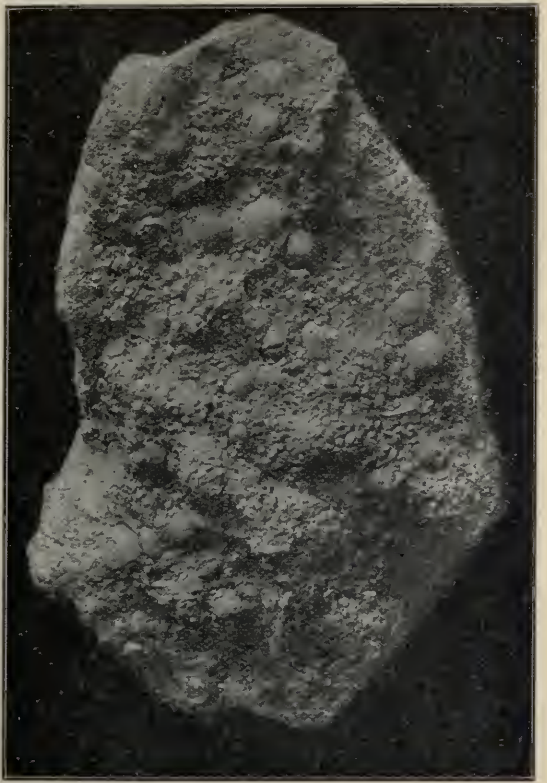

FIG. 5.

Block of Eocene limestone, showing the two forms of a species of *Nummulites*, constituting "a pair"; the larger named *N. biarritzensis*, the smaller *N. guettardi*, d'Arch. Specimen from Deir en Nakhl, Egypt, in the Brady Collection, Cambridge.

### *The Phenomenon of Dimorphism.*

This phenomenon was first recognised in the fossil nummulites which abound in the marine deposits of the Eocene period, and are represented by a single species living at the present day.

They are often so abundant that, as in the rock of which some of the Egyptian pyramids are built, their coin-like shells, whole or in fragments, constitute the main part of the deposit (Fig. 5). The shells are, in reality, not flat but biconvex discs, and the chambers, arranged in a spiral, are so disposed that the greater part of the cavity of each lies in the median plane, while the shell on either side of this plane is comparatively solid. They thus readily break, as the result of weathering or by artificial means, into plano-convex halves, which display a section of all the chambers from the centre to the periphery on their broken faces.

It has long been recognised that while the great majority of the specimens of nummulites occurring in a deposit attain a certain, moderate size, a few are found scattered through it, whose diameter far exceeds that of the others. On examining median sections of the smaller specimens it is usually found that the spiral series of chambers starts from a large and nearly spherical chamber readily visible to the naked eye, and occupying the centre of the shell, while in the larger specimens the spiral series is continued to the centre, where, in carefully prepared sections, it may be seen to take its origin in a spherical chamber of microscopic size (Fig. 6).

Although the two forms were thus found to be associated in the same beds, and to agree with one another closely except in the size to which they grow and the characters of the central chambers, they were given separate specific names, and attention was called to the puzzling occurrence of these associated pairs of species, a large and a small one, in various deposits.

Thus the names *Nummulites laevigata*, Lam., and *N. lamarcki*, d'Arch., have been given to two associated forms occurring in beds of the Middle Eocene formation. The former attains a diameter of 20 mm., while the latter does not exceed 3 or 4 mm. Small examples of *N. laevigata* are not to be distinguished by external characters from the associated form, but on splitting them open, the difference in their central chambers is at once apparent (Fig. 6). Sixteen pairs of similarly associated "species" belonging to the genera *Nummulites* and *Assilina* have been enumerated.

The possibility that the two associated forms might belong to the same species was, however, entertained by several observers, and the acceptance of this view was accelerated by Munier-Chalmas (26), who (in 1880) definitely formulated the conclusion that the species of nummulites are dimorphic, each appearing under two forms, a large one and a small one. He also expressed the opinion that the phenomenon of dimorphism would be found to be of general occurrence among the Foraminifera.

As already stated, the large forms with a small central chamber are much less abundant than the others, and it so happened that young individuals of this form did not come under Munier-Chalmas's observation. He was thus at first inclined to the view that the individuals of the two sets, although in some way distinct in nature, began life under one form, namely, that with a large central chamber. At a certain stage, it was supposed, the growth of one set of individuals was arrested, while in the members of the other set the walls of the large central chambers were absorbed, and growth was continued not only by the addition of chambers at the periphery in continuation of the series of those already formed, but also in a centripetal spiral towards the centre of the shell, filling the space originally occupied by the large central chamber.

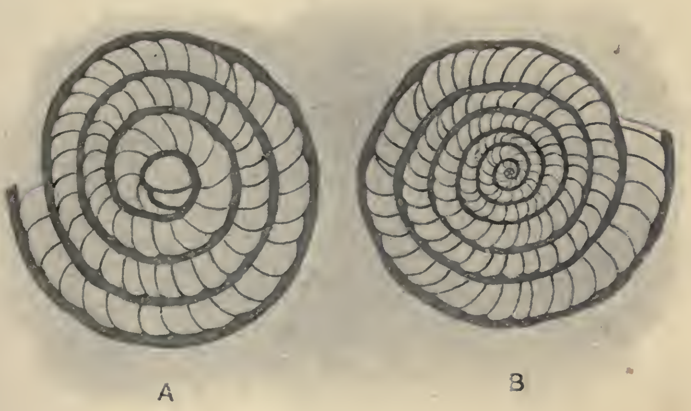

Fig. 6.

*Nummulites laevigata*, Lam. A, Central portion of a section of the megalospheric form ("*N. lamarcki*," d'A.); B, of the microspheric form. Both × 10. (After de la Harpe, 17.)

This idea of the relationship of the two forms was controverted by de la Harpe, who pointed out, expressing his own views and those of de Hantken, that young examples of the form with a small central chamber are known to occur, and also that differences may be detected not only at the central parts of the shells of the two forms of nummulites, but throughout the series of chambers. Thus it is often found to be the case that in the forms with a large central chamber (A, Fig. 6) the maximum size of the chambers subsequently added is attained early in the series of whorls, while in the others (B) the size of the chambers gradually increases to the last whorl.

While the view that one form results from the modification of the other was thus shown to be untenable, it was suggested that they might with more reason be regarded as representing the two sexes of a species. The authors did not, however, abandon the old idea of the specific distinctness of the two forms.

Investigation of other genera of Foraminifera has shown that the phenomenon of dimorphism is, as Munier-Chalmas expected, widely found among them.

The relation between the two forms will be best elucidated by examining the structure and life-history of a single species. For this purpose we will select *Polystomella crispa* (L.), the life-history of which is most completely known.

THE STRUCTURE OF POLYSTOMELLA CRISPA.—This is one of the most abundant of the littoral Foraminifera. It lives in shore pools and down to a depth of 355 fathoms, and ranges from Greenland in the north and Kerguelen Island in the south to the equator. It is very common on our own shores.

The test is biconvex and symmetrical about the median plane. The chambers are arranged in a spiral series, and are equitant, *i.e.* they bestride the chambers of the preceding convolution and overlap them at the sides, each being prolonged in what are known as *alar prolongations*, which extend towards the spiral axis of the test. Partly as the result of this overlapping, and partly because the axial region is filled in with canalicular shell substance, only the last convolution of chambers is visible externally.

On the terminal face of the last chamber, where this face joins the wall of the preceding convolution, a V-shaped line of pores (Fig. 7, *a*) is visible. These represent the aperture of the test, and are the main channels of communication between the terminal chamber and the exterior. At the posterior margin (*i.e.* the margin remote from the terminal face) of each chamber a number of pocket-like prominences, the *retral processes* (Figs. 7 and 8, *r*), project backwards, and are marked by ridges on the external surface. They end blindly, but are separated by pits, at the bottoms of which are the openings of branches of the canal system, which will be described later. The outer surface of

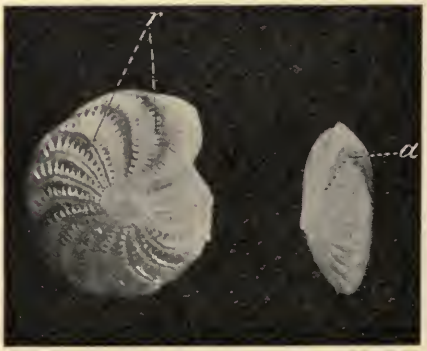

FIG. 7.

The test of *Polystomella crispa* (L.). × about 40. *a*, the line of terminal apertures; *r*, retral processes; between them are seen the pits by which branches of the canal system communicate with the exterior.

the shell is dotted over with minute tubercles (not visible in Fig. 7).

A keel-like thickening runs round the margin of the test, and in some specimens small spines, like the points of a spur, project from it at the places where the septa join the keel. These are more frequently present in the earlier than in the later convolutions.

The pores traversing the walls of the chambers are in this species exceedingly minute. They are hardly visible when the test is seen from without, but they may be detected when a broken piece of the wall is highly magnified and seen by transmitted light.

On examining the external characters of the tests of a number of Polystomellas, they are found to form a uniform series, presenting such gradations of size from small to large as may be seen, for example, in a sample of the shells of any Mollusc which contains young and old. If, however, a batch of living Polystomellas is killed by some reagent which dissolves the shell but preserves the protoplasm filling its chambers, the protoplasmic casts of the shells no longer form a uniform series but fall into two sets (Fig. 8).

In the great majority of them the series of chambers, when traced to the centre of the spiral, is seen to take its origin in a large spherical chamber, having a diameter generally between 60 and 100 $\mu$. In the others a small central chamber, with a diameter of about 10 $\mu$,[1] occupies the centre of the test, and the succeeding chambers of the series are at first correspondingly small, so that for a given diameter of test these specimens have a greater number of chambers than the others.

It is clear that though in *Polystomella* there is no marked difference in the size attained by the two forms, we have here the same phenomenon of dimorphism which is exhibited in the nummulites.

The large central chamber is known as the *megalosphere*, the small one as the *microsphere*, and the two sets of individuals of the species are known as the *megalospheric* and *microspheric* respectively. The numerical proportion of the two kinds of individuals probably varies with the season, but the megalospheric form is here also always the more abundant. In a large batch of several hundred specimens the megalospheric forms were found to be thirty-four times as numerous as the microspheric.

In the protoplasmic casts obtained in this manner the form and disposition of the chambers are well displayed. In the

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[1] The diameter of the microsphere varies in the specimens of *P. crispa* which I have seen from 6·5 to 13 $\mu$. That of the megalosphere from 165 to 35 $\mu$. These dimensions fall, however, a little short of the actual diameters of the chambers, owing to the shrinkage of the protoplasm produced by the reagents. When comparing the size of the microsphere in specimens preserved in this manner and in those examined by sections of the test, it is well to bear this cause of difference in mind.

The number given as the diameter of a central chamber, in this article, is to be understood as the mean between the long and short diameters as presented for observation in the specimen.

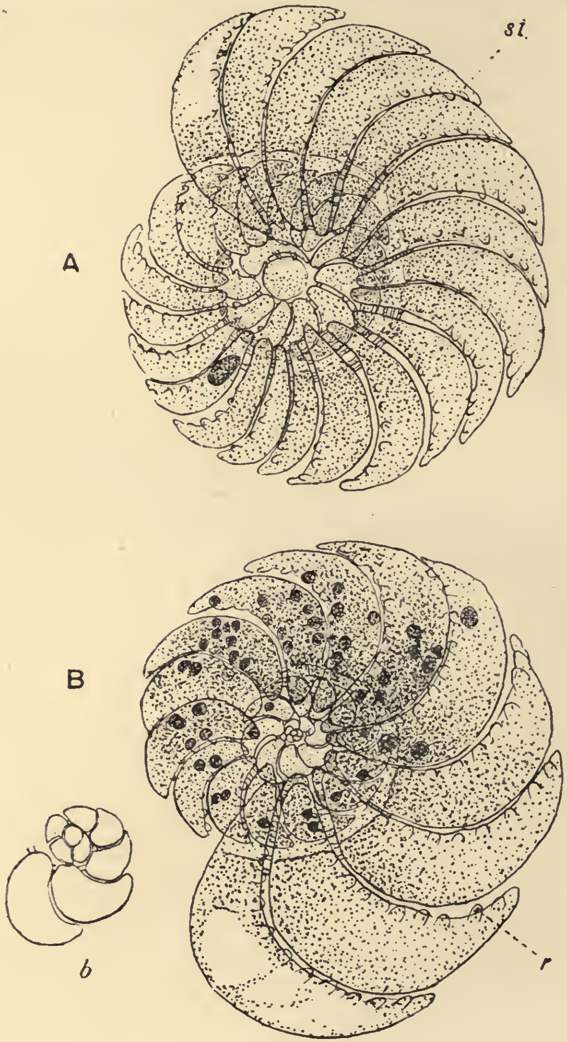

FIG. 8.

*Polystomella crispa.* A, the megalospheric, B, the microspheric forms, decalcified. *b*, the central chambers of the latter more highly magnified. The canal system is omitted in these figures for the sake of clearness. *r*, retral processes; *st*, communications between the chambers.

*megalospheric* form the retral processes characteristic of the genus are present in the chamber following the megalosphere (Figs. 8, A, and 11, *c*). In the first convolution of chambers the alar prolongations are hardly formed, but as the series is followed on, they project more and more at the sides, overlapping the chambers of the preceding convolutions; and as they increase the number of apertures between successive chambers, single in the earlier chambers, also increases (Fig. 8, A, Fig. 9, *st*), so that in the terminal chamber there is, as we have seen, a V-shaped row of pores leading to the exterior.

In the *microspheric* form the arrangement is similar in the later chambers, but in this form the retral processes are absent from the chambers of the earlier convolutions (Fig. 8, *b*).

The main trunks of the *Canal System* lie in the umbilical region.[1]

They consist of a spiral canal, on either side of the test, running parallel with and just internal to the lateral margins of the chambers—whether these are produced into alar prominences or not (*sp.c*, Figs. 9 and 11, *c*). Opposite the intervals between the chambers *meridional canals* (*m.c*) are given off, and run in the thickness of the septa, at some little distance from their outer margins, to meet one another in the median plane. From these numbers of short canals pass outwards, and, in the case of the outer convolution of chambers, open to the exterior, into the pits

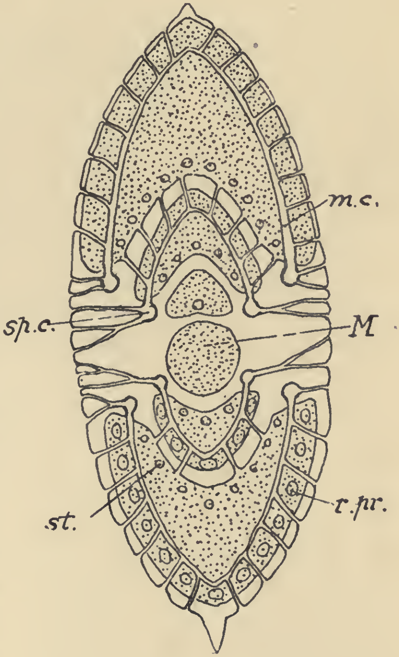

FIG. 9.

Diagram of a section through a megalospheric example of *Polystomella crispa*. It is represented as passing through the megalosphere but *between* the other chambers, in order to show the disposition of the canal system. *M*, the megalosphere; *m.c*, meridionial canal; *r.pr*, retral processes; *sp.c*, spiral canals; *st*, protoplasm traversing the apertures between the chambers. The dotted portion indicates the protoplasm filling the chambers, but the canal system is represented as empty. The numerous minute pores leading direct from the chambers to the exterior are omitted, and the shell substance is left blank.

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[1] The canal system is said by Carpenter to be imperfectly developed in *Polystomella crispa* (8, p. 282), and Möbius (25, p. 103) places *P. craticulata*, Fichte and Moll, in a new genus *Helicoza*, on the ground that it possesses a branched canal system, absent in *Polystomella*. In decalcified specimens of *P. crispa*, however, whose protoplasm has been coloured dark by osmic acid, it is easy to convince oneself of the existence of the system.

between the retral processes, before mentioned as visible on the surface of the test (Fig. 7). The short canals springing from the meridional canals of the inner convolutions open into the chambers of the convolution next external. The canal system is thus in communication with the chambers. In addition to the meridional canals, other branches spring from the spiral canals and pass to the surface in the umbilical region, traversing the thick mass of canalicular skeleton there deposited.

The course of the spiral canals is in some cases irregular, and they often break up into a network of sinuses. In the small specimen shown in Fig. 11, *c*, the spiral canal of one side is seen close to its origin, and a meridional canal is shown, between the second and third chambers; but I have been unable to trace the points of origin of the spiral canals.

On treating a batch of decalcified specimens with a stain such as picrocarmine, the *nuclei* appear, and again the two sets of individuals come into marked contrast. The megalospheric form possesses a single large nucleus, while the microspheric form possesses a number of small nuclei, distributed through its chambers (Fig. 8).

In *Polystomella crispa*, then, the megalospheric individuals are numerous, they have a large central chamber and a single large nucleus; while the microspheric individuals are comparatively scarce, they have a small central chamber, and many nuclei.

The existence of the phenomenon of dimorphism being verified, the question arises: How are the two forms related?

For an answer to this question we turn to the life-history, and what is known on this head will now be given.

LIFE-HISTORY OF POLYSTOMELLA CRISPA—*The Microspheric Form.*—The youngest specimens of this form that have been met with already contained many nuclei. Thus in one, described by Schaudinn (44, p. 92), with nine chambers, twenty-eight nuclei were present.

The nuclei are at first homogeneous bodies, but as the animals grow nucleoli make their appearances. The nuclei are irregularly scattered through the protoplasm, though they are not found in the terminal chambers. They are often grouped in pairs, and there is good evidence that they multiply by simple division (20, p. 419). The nuclei in the larger chambers are larger than those in the small chambers near the centre, and they may attain a diameter of 40-50 $\mu$.

In addition to these rounded nuclei, there are generally present in the protoplasm of the microspheric form abundant irregular strands of darkly staining substance, which are apparently given off by the nuclei. In some cases no definite nuclei are visible—

all the stained substance present being in the form of such irregular strands.

*Reproduction of the Microspheric Form.*—The first indication of the approach of the reproductive phase as seen in the living animal is a great increase in the number of the pseudopodia. They are so abundant that when the specimen is attached to the side of a glass vessel and seen by transmitted light, they form a conspicuous milk-white halo about the brown shell (Fig. 10, *a*). The halo is at first composed of clear hyaline protoplasm, but in a

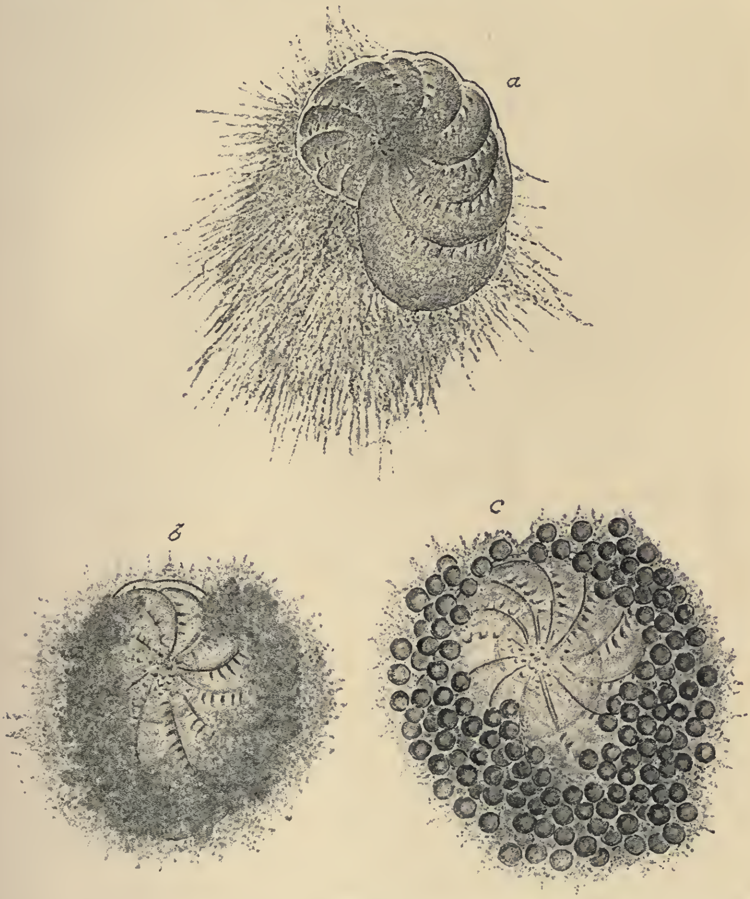

FIG. 10.

**_a-c_, stages in the reproduction of the microspheric form of _Polystomella crispa._ Drawn from photographs of one specimen attached to the side of a glass vessel.**

short time the coarse brown granules, hitherto contained within the test, begin to pass out, and ultimately the whole of the protoplasm, emerging from the test, is massed within the area covered by the halo and lies between the test and the supporting surface (Fig. 10, *b*). Here, after involved streaming movements, the protoplasm gradually and simultaneously separates into spherical masses of uniform size. The centre of each is occupied by a nucleus, with an area of clear protoplasm immediately surrounding it. A close network of delicate pseudopodia surrounds the spheres and forms a communication between them (Fig 10, *c*). In a short time each sphere secretes a calcareous shell, a single small aperture being left by which the pseudopodia pass out. After lying in close contact for some hours, the spheres rapidly and simultaneously draw apart from one another, and within half an hour from the beginning of the movement they are dispersed over a wide area, and each becomes the centre of a system of pseudopodia of its own, though for some time they are not completely isolated (Fig. 10, *d*).

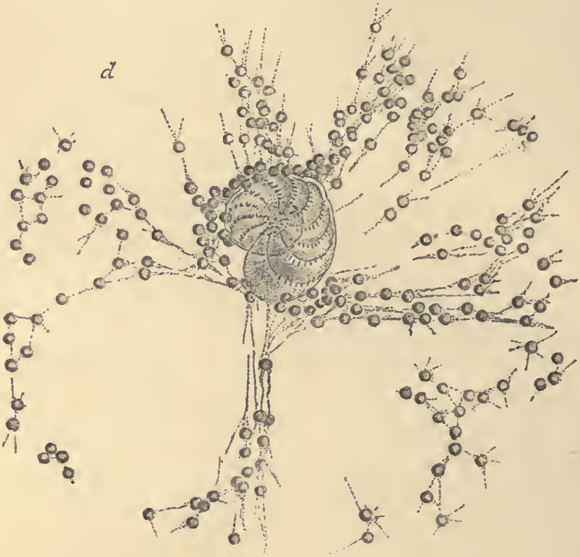

Fig. 10 (*continued*).

*d*, later stage in the reproduction of the specimen of *Polystomella crispa* represented in Fig. 10, *a-c*.

The whole protoplasm of the parent is used up in the formation of the brood of young, the shell being left empty. The process, from the first appearance of the halo to the dispersal of the young, is complete in about twelve hours.

In a short time the protoplasm which lies outside the aperture of each of the spheres secretes the wall of a second chamber of characteristic form, and the young individual is then clearly recognisable in size and shape as the two-chambered young of the megalospheric form (Fig. 11, *b*).

The nature of the parent which gives rise to this brood of megalospheric young is determined by decalcifying specimens which are entering on the reproductive phase, before the protoplasm has left the central chambers. In upwards of fifty cases thus examined the centre was found to be occupied by a microsphere. We have then, in this process, a transition from the microspheric to the megalospheric form.

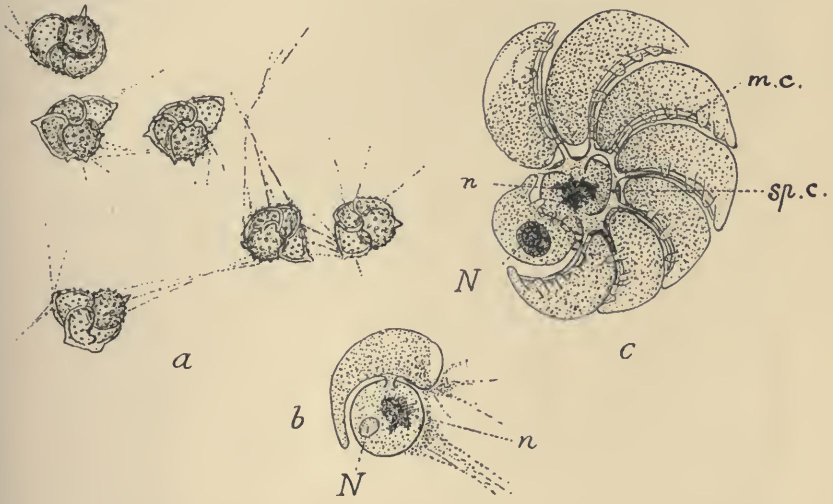

FIG 11

Young megalospheric individuals of *Polystomella crispa*. *a*, a group of six, two days after their formation. Four chambers are formed. *b*, a specimen with two chambers, decalcified and stained; *N*, the nucleus; *n*, irregular stained mass. *c*, a specimen with nine chambers, similarly treated; *N* and *n* as in *b*; *sp.c*, spiral canal of the canal system; in this specimen it becomes irregular near the last-formed chamber; *m.c*, meridional canal.

Schaudinn (44, p. 94), has found great variation in the size of the megalospheres produced by one parent, namely, from 10 to 120 $\mu$. He therefore holds that the two forms of *Polystomella*, though differing in their nuclear characters, are not always distinguishable by the size of the central chambers. He also finds (p. 93) that in some cases the shell of the young megalospheric form is not secreted until the spherical masses of protoplasm have wandered about for a long time.

The details of the reproductive process given above are those which I have invariably observed in specimens which were kept in clean sea-water.

In my first observations the water circulating in the tanks of the laboratory was used; and though I repeatedly saw the protoplasm emerge from the parent shell and break up into spheres, the development did not pursue a normal course. Again and again the spheres, after remaining separate for some hours, fused with one another, and finally the mass broke up into irregular globular bodies of very unequal size, which remained alive for days, but did not, in most cases, secrete a shell. It was not until fresh sea-water was used in the jars that I had the pleasure of witnessing the normal process of development.

In view of this experience, and of the fact that though I have examined some thousands of specimens of *Polystomella*, I have never met with a megalospheric form with a central chamber less than 34 $\mu$ in diameter, I am inclined to think that the great irregularities in size in the brood of young, and the small diameter of some of them, are the result of abnormal development.

In some genera, however, as stated below, the two forms cannot always be distinguished by the size of the central chamber.

*Nuclear Changes.*—When, in the reproduction of the microspheric form, the megalospheres first become isolated, the centre of each is occupied by a sharply-defined, round nucleus, about 7-8 $\mu$ in diameter, staining uniformly pink in picrocarmine. At this stage there is also diffused in the protoplasm a material taking a stain in this reagent; but in a short time the stained material, previously diffused, becomes aggregated in defined but irregular masses, which gradually draw together, and for a time frequently hide the nucleus from view. When two or three chambers of the young test have been formed the nucleus is again distinctly visible (Fig. 11, *b*, *N*), together with one or more irregular masses (*n*) formed by the closer aggregation of the previously diffused material. In many cases, though not in all, a mass apparently identical with the latter remains visible in or near the central chamber in specimens of the megalospheric form in advanced stages of growth; but it is, I believe, the round nucleus which was seen in the megalosphere at its first formation which becomes the nucleus ("principal kern") of the megalospheric form.

The relation between this nucleus and the nuclei and irregular strands of the microspheric parent has not been followed.[1]

*Growth and Reproduction of the Megalospheric Form.*—As the individuals of this form grow, and the number of their chambers is augmented, the nucleus likewise increases in size, and, leaving the megalosphere, it moves on through the chambers, becoming temporarily constricted as it passes through the narrow passages connecting them. In specimens fairly advanced in growth the nucleus is, as Schulze pointed out (64, *a*), usually found in or near the chamber which is numerically in the middle of the series.

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[1] I have not met with any evidence in support of Schaudinn's statement (44, p. 95) that the large nucleus ("principal kern") of the megalospheric form results from the massing together of the irregular strands of the microspheric parent.

In the cells of growing vegetable tissues the nucleus moves towards that part of the cell at which growth is most actively proceeding.[1] Thus in a growing root-hair the nucleus is found near the tip; in a young stellate hair, it lies at the point of junction of the rays. Its movement towards the regions of activity results, we must suppose, from a certain force impelling it in that direction, and its position when at rest is at the point where the impelling forces, resulting from the activities of the protoplasm in different parts of the cell, are in equilibrium.

In the forms of Foraminifera in which the nucleus is single it appears that its position is likewise dependent on the disposition of the protoplasm. Thus in the megalospheric forms of *Cycloclypeus* and *Orbitolites complanata* the nucleus is found in or near the central chamber, where, owing to the cyclical growth in these genera, the attractions, due to activity at the periphery, are in equilibrium. In the forms with spiral arrangement the nucleus moves on through the series of chambers as growth proceeds. In *Polystomella*, however, the nucleus of the megalospheric form always lags some distance behind the point at which, judging from the disposition of the bulk of the protoplasm, we should expect the attractive forces to be in equilibrium.

At the earliest stage at which it has been recognised the nucleus appears to be a homogeneous body. As it grows, round nucleoli make their appearance, and these are comparatively large in young specimens, and decrease in size while they increase in numbers as growth proceeds.

Sections through the nucleus of specimens fairly advanced in growth show a well-defined nuclear wall, a reticulum with finer or coarser meshes occupying the interior, and rounded nucleoli at the nodal points of the reticulum. Minute granules may often be detected in the strands of the reticulum.

It appears that throughout the vegetative phase of the megalospheric form small fragments are separated off from the nucleus, and they may often be seen as irregular bodies, sometimes containing nucleoli, lying in the neighbourhood of the nucleus, or in the chambers through which it has passed in its passage onwards from the megalosphere.

Towards the end of the vegetative phase of the life-history of the megalospheric form the nucleus loses its regular outline and its power of receiving stains, and finally disappears. In such specimens it may often be observed that additional passages have been opened up, by the dissolving action of the protoplasm on the shell substance, between adjoining chambers of inner and outer convolutions, so that the inner chambers are placed in more direct communication with the outer, and so with the exterior.

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[1] Cp. Haberlandt's researches, quoted by O. Hertwig, *Die Celle und die Gewebe* i. p. 259.

*Reproductive Phase of the Megalospheric Form.*—In specimens in which the large nucleus has disappeared hosts of minute nuclei may be found, scattered uniformly or in groups through the protoplasm.

Presumably these are derived from constituents of the principal nucleus, and possibly of the small nuclear fragments as well, but their precise relation to these bodies has not been followed.

When the nuclei are evenly distributed the protoplasm breaks up into minute rounded masses, the centre of each being occupied by a nucleus. Division of these nuclei by karyokinesis now occurs, and is simultaneous or nearly so throughout the organism, and this is followed by a second division of the protoplasm to form rounded bodies about 3-4 $\mu$ in diameter, each containing one of the daughter nuclei (Fig. 12). At a later period the contents of the shell issue as active zoospores of approximately uniform size, which swim rapidly by means of flagella.

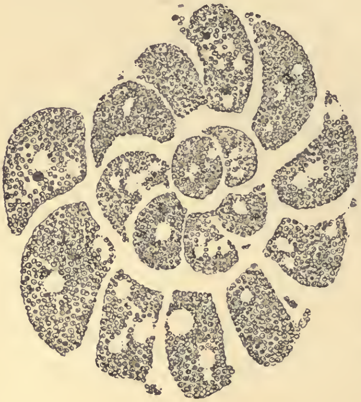

Fig. 12.

Section through a specimen of the megalospheric form of *Polystomella crispa*, in which the contents are divided up into zoospores. × 160.

It is to be noted that, as in the case of the reproduction of the microspheric form, the whole of the protoplasm of the parent is used up in the production of the zoospores.

Though the zoospores have been seen issuing from the shell, their precise characters, when ripe, have not been accurately described; nor have we as yet direct evidence as to their fate.

That there is a close relation between the zoospore and the microsphere is suggested by the fact that there is no great difference in size between these structures, the diameter of the former, before their escape from the parent shell, being 3-4 $\mu$, and that of the latter about 10 $\mu$. A further piece of evidence tending in this direction is furnished by an observation of Schaudinn's (44, p. 92). In an aquarium containing abundant Polystomellas, Schaudinn suspended coverslips by means of threads, so arranged that the lower borders of the coverslips were separated by about 2 cm. from the stratum covering the bottom of the aquarium. After two days young examples of the microspheric form were found on the coverslips. Now throughout the vegetative phases of its life *Polystomella* crawls over the surface of submerged objects, by means of its pseudopodia, but is incapable of swimming freely; and as the depth of 2 cm. far exceeds the distance to which the pseudopodia of so young a specimen are likely to extend, the colonisation of the coverslips by the microspheric form under these conditions points to the existence of a free swimming stage prior to the vegetative stage in which the young forms were found. Such a stage is supplied by the free swimming zoospore.

The results furnished by direct observations on the life-history of *Polystomella* may be summarised in two statements:—

*The microspheric form terminates its existence by becoming transformed into a brood of megalospheric young.*

*The megalospheric form terminates its existence by becoming transformed into minute zoospores of uniform size.*

Before discussing the bearing of these results on the relationship of the microspheric and megalospheric forms, it will be convenient to consider some facts in another life-history, that of *Orbitolites complanata.*

LIFE-HISTORY OF ORBITOLITES COMPLANATA.—The main features of the structure of this species are described below (p. 104 and Figs. 36 and 37). For the present purpose it will be sufficient to point out that the mode of growth is, except in the early stages, cyclical, concentric rings of small chambers being added at the margin of the disc-shaped test, and that the tests are biconcave. In the *microspheric* form the central region is thin, being built up of the microsphere and the small chambers or "chamberlets" which succeed it.

In the *megalospheric* form the centre of the shell is thicker owing to the presence of the "primitive disc" (Figs. 37, A, and 38). This consists of the megalosphere, a spiral passage, and of the very large crescentic chamber, which nearly surrounds the other constituents of the primitive disc. The outer margin of the crescentic chamber is perforated by pores, by which it opens into the innermost ring of chamberlets.

*Reproduction.*—The production of megalospheric young by a microspheric parent has been repeatedly observed (4 and 20, and Fig. 36, *b*). In the later stages of the growth of the parent spacious *brood chambers* are formed at the periphery of the disc, and in the reproductive phase the protoplasm is withdrawn from the small chambers internal to them and massed in the brood chambers, where it breaks up to form the brood of young. On their escape, which is effected by the breaking down of the outer walls of the brood chambers, presumably under the dissolving action of the protoplasm of the young, the test of each young individual has already the structure of the "primitive disc" which is found at the centre of the megalospheric form (Figs. 37, A, and 38).

This process is clearly comparable with the formation of the megalospheric young by a microspheric parent which we have followed in *Polystomella*, the chief difference consisting in the fact that the young are formed in peripheral brood chambers and not outside the test of the parent.

By analogy with *Polystomella* we cannot doubt that megalospheric parents give rise to zoospores. Specimens of *Orbitolites* have, however, been found (and the corresponding phenomenon has also been observed in several other genera) in which a brood of megalospheric young occupies the peripheral chambers of a test, the centre of which is formed by a primitive disc, and which is therefore megalospheric (20, p. 435). Hence we must conclude that in these cases the megalospheric form may be repeated, possibly more than once, before a brood of zoospores is produced. The behaviour of the nucleus under these conditions has not been closely followed.

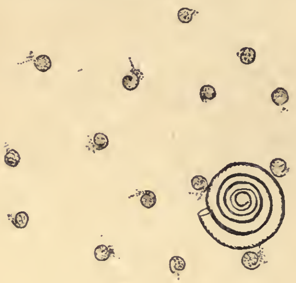

FIG. 13.

*Cornuspira involvens*, Reuss. The contents of a megalospheric form have emerged from the shell and divided up into a number of young, which are also megalospheric. In both parent and young the megalosphere was about 80 μ in diameter. × 30. Cp. Fig. 20.

Fig. 13 illustrates a similar repetition of the megalospheric form in the case of *Cornuspira involvens*.[1]

### *The Relation between the Microspheric and Megalospheric Forms.*

With the evidence furnished by the life-histories of *Polystomella* and *Orbitolites* we may now return to the question of the relationship of the megalospheric and microspheric forms.

The earliest view held on this subject, that they represented two species of a genus, is at once disposed of by the fact that the megalospheric form is the offspring of the microspheric.

The next suggestion was that the two forms represent the two sexes.

To this, two objections may be made on general grounds. (1) The difference between them is most marked at the beginning of their growth, when they consist only of the central chambers, the microsphere or the megalosphere, while males and females arise from eggs which are, so far as observation has yet advanced, similar, and are most differentiated when adult. (2) Although the differentiation of male and female gametes is known in several groups of the Protozoa (*Sporozoa*, *Ciliata*, *Flagellata*), a differentiation of the parent organisms which produce the gametes, which would be the phenomenon comparable with the sexual dimorphism of the Metazoa, is unknown among the Protozoa.

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[1] In his preliminary paper Schaudinn states (44, p. 96) that the megalospheric generation may also be repeated (though rarely) in *Polystomella*, and that in such an event no principal nucleus is formed by the megalospheric parent. As Rhumbler remarks in his notice of Schaudinn's paper (*Zool. Centralblatt. Jahrg.* 2 (1895), p. 453, footnote), it is difficult to see how this result can be reached, for the shell of *Polystomella* is too thick to allow the nuclear condition to be observed during life.

But apart from *a priori* objections, it may be well to try how the ascertained facts of the life-history fit this hypothesis. The megalospheric form, producing zoospores, would evidently on this view represent the male, while the microspheric form, producing the large megalospheres, might be regarded as the female. It might be supposed, the fate of the zoospores being unknown, that they unite with and fertilise the megalospheres. But while the origin of the megalospheric form, the supposed male, is thus accounted for, that of the microspheric form, the supposed female, remains unexplained, and as the whole of the protoplasm of the parent is, to all appearance, used up in the brood of megalospheric young, the hypothesis is at fault. Moreover, in *Orbitolites*, *Cornuspira*, and other genera the megalospheric form may also give rise to a brood of megalospheric young, a proceeding foreign to the nature of a male organism. Hence neither of the forms of the species conforms to the character assigned to it by the hypothesis: the microspheric form, the supposed female, in that it does not produce "females"; the megalospheric form, the supposed male, in that it does in some instances produce "males."

A third hypothesis is in harmony with what we know in other groups of the Protozoa, and fits the ascertained facts. It is that the two forms represent alternating or recurring generations in a life-cycle. The individuals of the microspheric form reproduce asexually by the multiple fission of their protoplasm to form broods of megalospheric young. The individuals of the megalospheric form may undergo, in some genera, a similar process, but ultimately a megalospheric individual is produced whose protoplasm divides into zoospores.

How is the gap between the zoospore and the microsphere filled?

That they are closely related is suggested, as stated above, by their approximation in size, and by the indication, afforded by the colonisation of Schaudinn's coverslips, of a free swimming stage preceding the vegetative phase of the microspheric form. Another remarkable fact bearing on the matter is the scarcity of the microspheric form in comparison with the megalospheric, a scarcity all the more striking when it is borne in mind how far more numerous are the zoospores produced by one megalospheric individual than the members of a brood of megalospheres.

The analogy of other life-histories would lead us to suppose that at some point in the cycle a sexual process, the conjugation, with nuclear fusion, of two organisms, occurs, and the life-history of *Trichosphaerium sieboldi*, Schn., which has lately been worked out by Schaudinn (47), to whom so much of the recent advance in our knowledge of the life-history of the Protozoa is due, appears to afford a very appropriate parallel. This form is not included in the Foraminifera, but is a somewhat aberrant member of the allied group—the Lobosa. The main features of its life-history are, however, remarkably similar to those of *Polystomella.*

The individuals are rounded multinucleated masses of protoplasm not contained in a definite shell, though surrounded by a gelatinous envelope. They form a dimorphic series, the members of which recur in a cycle of generations. In those of one generation, which may be called by Haeckel's term *Amphionts*, reproduction occurs by the simultaneous division of the protoplasm about the nuclei to form spherical uninucleated masses, which emerge and grow into the members of the other generation—the *Mononts.* These in their turn break up, after subdivision of their nuclei, into zoospores. The zoospores are biflagellate organisms, and are all alike.

While the zoospores from the same parent will not unite with one another, those from different parents conjugate readily. In this process, which has been carefully followed by Schaudinn, the nuclei of the two gametes unite, their flagella drop off, and the *zygote* so produced, absorbing fluid, undergoes a considerable increase in size, so that in a few hours its diameter is more than doubled. The zygote shortly afterwards secretes a gelatinous envelope, and the characters of the full-grown individual of the amphiont generation are gradually acquired. The multinucleate condition results from successive mitotic divisions, beginning with that of the nucleus of the zygote.

In *Hyalopus dujardinii*, which may be regarded as a member, though an aberrant one, of the Foraminifera, Schaudinn (43) has also observed the conjugation of zoospores, but in this case the process occurred between members of the same brood.

If we assume that a similar conjugation of zoospores occurs in *Polystomella*, the facts above alluded to are at once explained.

The fusion of two zoospores (4 $\mu$ in diameter), and the subsequent expansion of the zygote by the absorption of water before the secretion of a shell, might well form a body of the size of the microsphere (about 10 $\mu$); the free locomotive stage prior to the settling down of the microsphere, indicated by Schaudinn's experiment, is supplied; and the comparative rarity of the microspheric form is explained on the supposition that, as in *Tricho-*

*sphaerium*, the meeting and conjugation of zoospores from different parents is necessary for the production of a microsphere.

It is very desirable that the conclusion should be confirmed by direct observation, but, meanwhile, it seems not premature to admit that it is probable that the microsphere arises from the conjugation of zoospores.

We may conclude, then, that the microspheric and megalospheric forms of the Foraminifera represent alternating or recurring generations in a life-cycle. While the megalospheric generation arises asexually, either from a microspheric or a megalospheric parent, it is probable that the microspheric generation arises sexually—*i.e.* by the conjugation of two similar zoospores.

Representatives of the two generations have been recognised in species belonging to the following genera of Foraminifera :—

ORDER 1. **Gromiidea** (?).[1]
( „ 2. **Astrorhizidea.**[2])
( „ 3. **Lituolidea.**)
„ 4. **Miliolidea.**

Family MILIOLINIDAE.—*Cornuspira* (24, 1898, p. 612); *Spiroloculina* (57, p. 201); *Biloculina* (27, p. 863); *Sigmoilina* (*Planispirina*, pars), Schl. (53, p. 106); *Triloculina* and *Quinqueloculina* (27, pp. 863 and 1598); *Massilina* (57, p. 218); *Adelosina* (52, p. 91); *Idalina* and *Periloculina* (28); *Lacazina* (27).

Family HAUERINIDAE.—*Planispirina*, Seg. (56, p. 194).

Family PENEROPLIDIDAE.—*Peneroplis* and *Orbiculina* (this article), *Orbitolites* (4, p. 693, and this article); *Meandropsina* (59).

Family ALVEOLINIDAE.—*Alveolina* (51, p. 526).

ORDER 5. **Textularidea.**

Family TEXTULARINAE.—*Textularia* and *Spiroplecta* (this article).

(ORDER 6. **Chilostomellidea.**)
„ 7. **Lagenidae.**

Family NODOSARIIDAE.—*Nodosaria* and *Dentalina* (51, p. 526); *Frondicularia* (15, p. 480); *Cristellaria* (?) (5, p. 45).

Family POLYMORPHINIDAE.—*Siphogenerina* (*Sagrina*) (50, p. 21).

(ORDER 8. **Globigerinidea.**)
„ 9. **Rotalidea.**

Family ROTALIDAE.—*Rotalia* (51, p. 526, and 20, p. 436); *Truncatulina* and *Calcarina* (20, pp. 436 and 437).

Family TINOPORIDAE.—*Polytrema* (23).

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[1] The cases of *Hyalopus* and *Mikrogromia* are considered below.

[2] In the orders included in brackets I have not succeeded in finding a record of the existence of dimorphism.

### ORDER 10. **Nummulitidea.**

Family FUSULINIDAE.—*Fusulina* (58, p. 1).

Family POLYSTOMELLIDAE.—*Polystomella* (20, p. 415).

Family NUMMULITIDAE.—*Operculina* (this article); *Amphistegina* (51, p. 526); *Nummulites* and *Assilina* (26, p. 300); *Heterostegina* (this article); *Cycloclypeus* (10, p. 21, and this article); *Orbitoides* (31, p. 258, and 61, p. 463); *Miogypsina* (60, p. 328).

Thus the phenomenon of Dimorphism, the occurrence of members of a species under two forms—the megalospheric and microspheric—is widely spread among the orders of the Foraminifera, and where it is found it affords clear evidence of alternating or recurring generations in the life-history of the species exhibiting it.

## REVIEW OF THE STRUCTURE AND LIFE-HISTORY DISPLAYED IN THE ORDERS OF THE FORAMINIFERA.

As the attention of the many workers who are occupied with this group is turned to the subject, the list of dimorphic forms will, no doubt, be greatly extended; but there are indications in the descriptions already published of phases in the life-history of some forms, especially in that borderland occupied by the simpler Foraminifera, which depart in a greater or less degree from those described in *Polystomella* and *Orbitolites;* and we may now take a survey of the features of life-history which have been described in the different groups, and of the more interesting modifications in the form of the test, which, as we have seen, is found to be more or less dependent on the phase of the life-history of the organism which secretes it.

In chambered tests, in which the walls of the first formed chamber remain unaltered throughout growth, evidence of the mode of origin of the individual, whether as a megalosphere or a microsphere, is furnished by the structure of the test. But in the great majority of the Gromiidea and Astrorhizidea, the tests expand to accommodate the increase by growth (cp. p. 54), and all indications of the size of the test when it was first secreted are obliterated. Hence we are deprived in them of part of the evidence on the course of the life-history which we have in other groups, and we must rely on the characters furnished by the soft parts of preserved specimens, or on direct observation of the living animals.

From the evidence which we have, however, it is not clear that the course of the life-history of some members of these orders is the same as that of the dimorphic Foraminifera above described.

### ORDER **Gromiidea.**

In *Euglypha* (Fig. 3) multiplication, by division into two, occurs as follows.[1] The specimen which is about to divide secretes fresh shell plates, which are at first dispersed in the protoplasm about the nucleus. The pseudopodia are withdrawn, and the protoplasm is extruded beyond the mouth of the test in a rounded mass. This grows until it assumes a size equal to that of the test from which it protrudes, and the newly-formed plates are disposed on the surface to form a new test. The nucleus divides by karyokinesis, half going to each end of the mass, and division of the protoplasm follows, one part remaining in the old shell and the other in the new one.

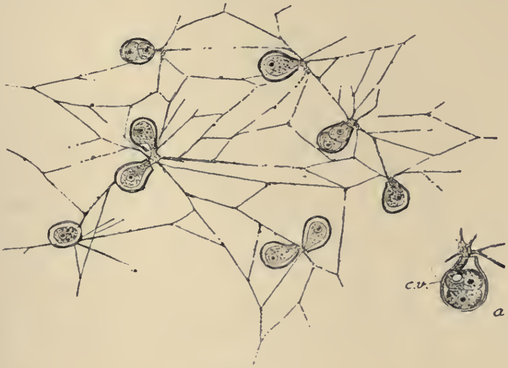

FIG. 14.

Colony of *Mikrogromia socialis* in the diffused condition. *a*, an individual in process of multiplication by transverse fission. *c.v*, contractile vacuole. Two of the members of the colony are seen to be undergoing the same process.

Blochmann (2) has described a process in which, after the division of the nucleus, the protoplasm was withdrawn from the newly formed shell, and this, together with the daughter nucleus remaining in it, was cast off. It is suggested that this may be comparable with the extrusion of parts of the nucleus observed in some other Protozoa and in polar-body formation. But in view of the fact that the new shell was cast off, as well as the daughter nucleus, this interpretation appears, to say the least, forced.

A temporary fusion of the protoplasm of two or more individuals, apparently without fusion of nuclei (plastogamy), was observed by Blochmann, and in one instance a new individual was apparently formed by the conjugation of two. In this case it was supposed that the nuclei had united (karyogamy) as the new individual was uninucleate.

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[1] The process was first described by Gruber (16), and followed out in detail by Schewiakoff (48).

Encystment also occurs in *Euglypha*, but what the subsequent stage may be is unknown.

*Mikrogromia socialis*, first described by Archer,[1] and afterwards more fully by R. Hertwig (18), is a fresh-water form, occurring in colonies, the members of which are united by their pseudopodia. The colonies are sometimes globular and compact (*Cystophrys* stage), sometimes diffused (Fig. 14), and in the latter condition present an interesting resemblance to a brood of young megalospheric individuals of *Polystomella* in a stage of dispersal (Fig. 10, *d*).

The growth of the colony results from the partial longitudinal fission of the members into two (or three), one (or two) of the products of fission escaping, secreting a new test, and taking its place in the colony. Hertwig also observed the production of young individuals, arising by transverse fission (Fig. 14, *a*). Of the two bodies so formed one remains in the test, continuing the vegetative phase of the parent, the other becomes free, and, in some cases, swims away as a biflagellate organism. In other cases, however, the flagella were not observed, being replaced by pseudopodia, resembling those of *Actinophrys*. The further history of the young thus produced was not followed. Assuming this to be a normal phase of development of *Mikrogromia*, it appears to be without a parallel in the life-history of *Polystomella*.

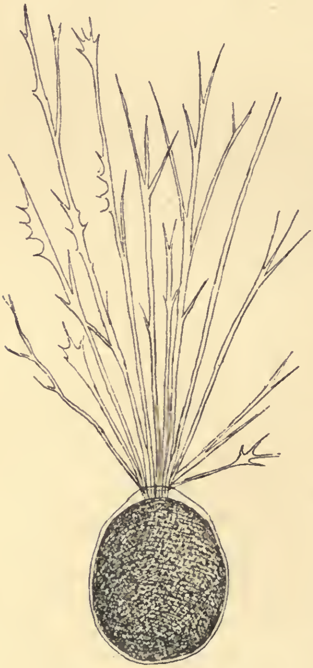

FIG. 15.

*Hyalopus (Gromia) dujardinii.* × 40. (After M. Schultze.)

*Hyalopus dujardinii*, Schaudinn (=*Gromia dujardinii*, M. Schultze) is a marine form distinguished by the hyaline and nongranular character of its pseudopodia, and by the absence of anastomoses between their branches. The main body of the protoplasm is covered by a chitinous envelope, and contains large brown rounded granules and many nuclei. In the condition in which it

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[1] Provisionally as two species, *Cystophrys haeckeliana* and *Gromia socialis* Archer (1).

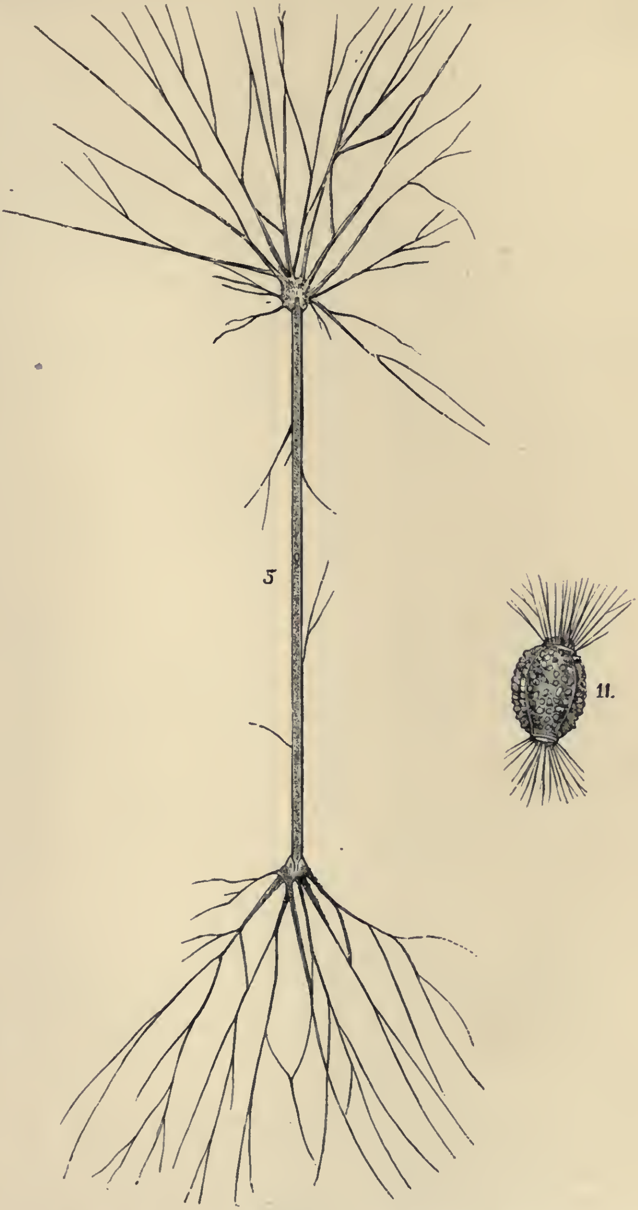

FIG. 16.

5, *Shepheardella taeniformis*, Siddall, × about 15. (After Siddall, *Q.J.M.S.*, vol. xx.) The nucleus is seen nearly opposite 5. 11, *Amphitrema wrightianum*, Archer, × about 210. (After Archer, *Q.J.M.S.*, N.S. vol. ix. 1869.)

was described by M. Schultze (64, p. 55), the shape is oval, and there is a single orifice (Fig. 15), but Schaudinn finds (43) that when living amongst the stems of algae, it loses its oval shape and assumes a branching form, new mouths being developed at the ends of the branches. Such branched forms may attain a length of 5 mm.

Two modes of reproduction were observed. One is by a process of fission, the body slowly dividing into two or three parts, sometimes of unequal sizes; the other is by the formation of zoospores. In the latter process the pseudopodia are retracted and the whole protoplasm divides up into oval or pear-shaped bodies, 5-8 $\mu$ in diameter, containing a nucleus 3-6 $\mu$ in diameter, a vacuole, and a conspicuous granule. They swim by means of a single flagellum 30-38 $\mu$ in length.

The zoospores conjugate in pairs, but in this case the conjugation is, according to Schaudinn, between members of the same brood. The further history of the zygote could not be followed.

The formation of the zoospores of *Hyalopus* is evidently comparable on the one hand with the reproduction of *Trichosphaerium* which gives rise to the "amphiont" generation, and on the other hand with the reproduction of the megalospheric form of *Polystomella.*

A similar mode of reproduction to the slow process of fission of *Hyalopus* has been seen in *Lieberkühnia* and *Lecythium*, the division of the protoplasm involving that of the envelope. Whether this is to be compared with the production of the brood of melagospheres by the multiple fission of the microspheric parent, or to the similar slow fission which occurs in *Trichosphaerium* in addition to the multiple fission of the "amphiont" parent, it appears to be at present impossible to decide. Many of the Gromiidea have a single orifice to the test, as in *Gromia* and *Euglypha* (Figs. 1 and 3). *Shepheardella* and *Amphitrema* have two orifices, situated at either end of a median axis (Fig. 16, 5 and 11).

### ORDER **Astrorhizidea.**

In *Saccammina*, and some other members of the Astrorhizidea in which growth is accompanied (as explained above, p. 54) by expansion of the test, no evidence on the phase of life-history represented, is furnished by its structure. But in other genera, such, for example, as *Hyperammina*, in which the tests grow not by expansion, but by addition, a large globular chamber is sometimes found at the commencement (Figs. 17, *d*, and 18). Such forms may well represent a megalospheric generation. There is, however, no evidence at present of the microspheric forms corresponding to them.

Rhumbler has made a careful investigation (33) of the nuclear characters of *Saccammina sphaerica* (Fig. 17, *b*). He found that among the 286 specimens which he examined, a single nucleus was present in all but one (which had two nuclei, and was regarded as abnormal), and the phases presented by the nuclei fell into a continuous series. They correspond with those of the nucleus of the megalospheric form of *Polystomella*. The nucleus increases in size with the growth of the organism, and the nucleoli ("binnen körper"), at first large and few, increase in number and diminish in size. Finally (Pl. 23, Fig. 67) the nuclear membrane breaks, and linin threads containing chromatin grains are dispersed in the protoplasm. From these later nuclear phases it appeared that some process of reproduction was imminent, but none was observed. The formation of zoospores by the Foraminifera was at that time unrecognised, and Rhumbler

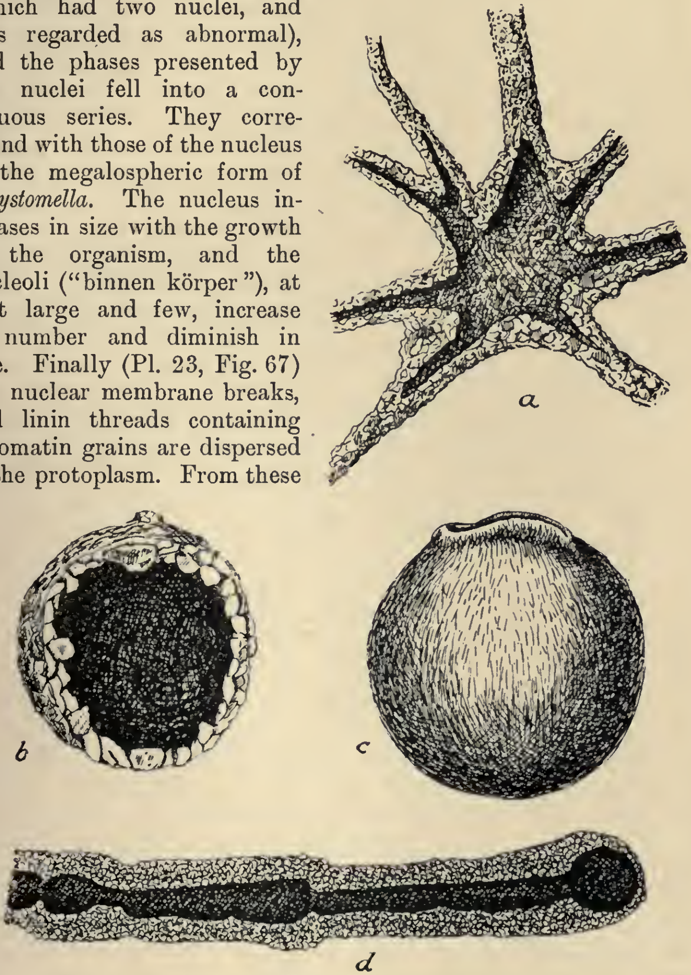

Fig. 17.

*a*, *Astrorhiza limicola*, Sandahl., × 6. *b*, *Saccammina sphaerica*, M. Sars, ×12. *c*, *Pilulina jeffreysii*, Carpr., × 12. *d*, *Hyperammina subnodosa*, Br., × 7. In *a*, *b*, and *d* the test has been laid open. (From Brady, "*Challenger*" *Report*.)

was surprised at finding no indication, notwithstanding the abundant material at his command, of the formation of a brood of young resembling the parent. On the analogy of the life-history of *Polystomella*, the absence of such indications appears in no way remarkable, for such a nuclear history is associated, as we have seen, with the production of zoospores.

The only difficulty in applying this analogy arises from the fact that no indications were found of a form of *Saccammina* with a different nuclear history, corresponding with that of the microspheric generation of *Polystomella*.

It is, of course, possible that the microspheric form, although occurring in nature, did not happen to be represented among the specimens examined; but however this may be, it is clear that we are not at liberty to assume the existence of a microspheric form in *Saccammina*. Hence, in the absence of other evidence bearing on the point, the Astrorhizidea cannot at present be admitted into the list of dimorphic Foraminifera.

In *Haliphysema tumanowiczii* (Fig. 19) Lankester (19) described numbers of "egg-like" bodies, varying in diameter from $\frac{1}{1500}$ to $\frac{1}{500}$ inch, scattered through the protoplasm. They appeared to be nucleated, and, in some cases, in process of division. It was surmised that they might be concerned in reproduction. Further information on the nature of these bodies would be very acceptable, but the possibility appears not to have been excluded that they are symbiotic or parasitic organisms similar to those which abound in the protoplasm of *Orbitolites complanata*.

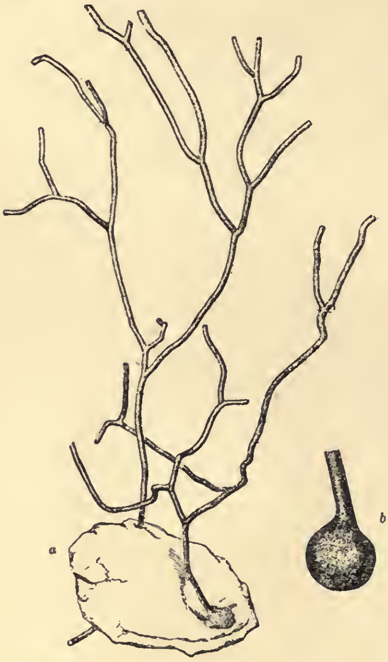

Fig. 18.

*Hyperammina arborescens*, Norm. *a*, two specimens growing attached to a stone, × 20; *b*, initial chamber of another specimen. (After Brady.)

### ORDER **Lituolidea.**

This order consists of arenaceous forms which are "isomorphic" with genera belonging to several of the other orders; and by many authors the order is broken up, and its genera associated with the calcareous forms which they resemble. In some cases (*e.g. Cornuspira*, *Nodosaria*, *Rotalia*) the latter are, as will appear below, dimorphic, so that we should expect their "isomorphs" to be so likewise; but though this is very probably the case, I am aware of no direct evidence on the matter.

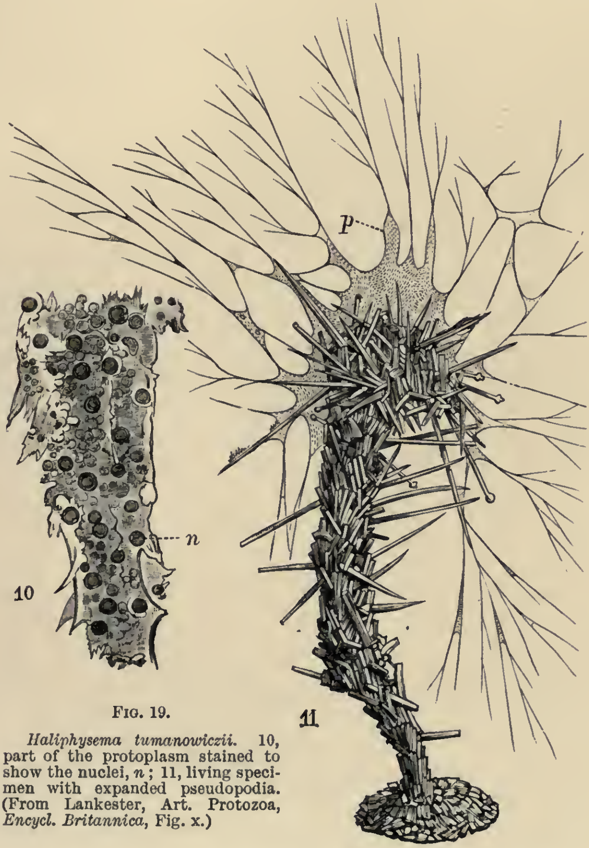

FIG. 19.

*Haliphysema tumanowiczii.* 10, part of the protoplasm stained to show the nuclei, $n$; 11, living specimen with expanded pseudopodia. (From Lankester, Art. Protozoa, *Encycl. Britannica*, Fig. x.)

A process of reproduction is recorded by Schaudinn (42) in *Ammodiscus gordialis*, P. and J. The protoplasm divides within the parent test into some 50-80 young, which become invested with a chitinous envelope, together with siliceous particles previously taken into the protoplasm.

## ORDER **Miliolidea.**

On coming to the Miliolidea we have a large body of evidence on dimorphism, thanks in great measure to the careful investigations of Schlumberger, by whom, either alone or in conjunction with Munier-Chalmas, the foundations of our knowledge on the dimorphism of the tests of Foraminifera have been laid. The tests will first be described, the nuclear characters and such details of the life-history as are to hand being given at the end.

Family *Miliolinidae.*—Before considering the phenomena of dimorphism in this family, it is necessary to describe the characteristic structure of the test in certain forms.

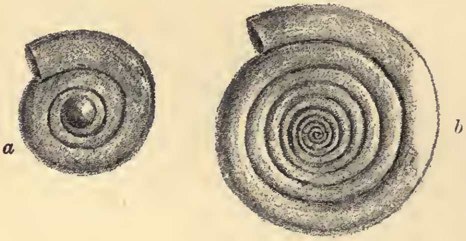

FIG. 20.

*Cornuspira involvens*, Reuss. *a*, the megalospheric form, × 90. *b*, the microspheric form, × 50. (From Brady, Parker, and Jones, *Trans. Zool. Soc.* vol. xii. Pl. 40, Figs. 1 and 2.)

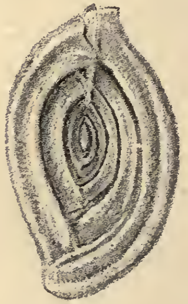

FIG. 21.

*Spiroloculina limbata*, d'Orb., × 30. (After Brady.)

The simplest type is met with in *Cornuspira.*

The whole of the test except the central chamber (which presents a well-marked difference in size in the two forms, Fig. 20) consists of a continuous tube, gradually increasing in diameter as it is followed away from the centre, but without any constrictions dividing it into separate chambers. In both forms it is disposed in a closely-wound spiral lying in one plane, so that a section in this plane would divide the test symmetrically.

In the genus *Spiroloculina* the arrangement is somewhat similar, but here the tube is divided into distinct chambers, each of which ends in a contracted mouth with an everted lip. The chambers increase successively in length, and are so disposed that each occupies half a turn of the spiral. It results from this arrangement that the mouths of the chambers are directed alternately in opposite directions, and each chamber is applied to that which is next but one before it in the series. A straight line, which passes through the central chamber and the mouths of all the chambers which succeed it, has been called the *axis of construction*. The spiral formed by the series of chambers is not quite regular, as is the case in *Cornuspira*; for while each chamber is gently curved, there is a sharp bend where one chamber communicates with another. Hence the test is elongated in the axis of construction. In *Spiroloculina* the chambers are disposed in one plane, and the width of each is only slightly greater than that of its predecessor, so that all the chambers are exposed on the two flat faces of the test (Fig. 21).

In all but the earlier chambers of the microspheric forms the arrangement characteristic of the genus *Biloculina* is essentially similar, but there is a marked difference in the shape and appearance of the test owing to the great width of the chambers. Each is so wide that its margins are in contact with those of its predecessor, and overlap them at the sides (Figs. 22, *a*, and 24). It results from this arrangement that the two last chambers enclose those previously formed, and they alone appear in the contour of the test. As in the preceding genus a median longitudinal section through the last chamber divides the whole series of chambers into symmetrical halves. As will appear later, the microspheric form of *Biloculina* departs considerably from this arrangement.

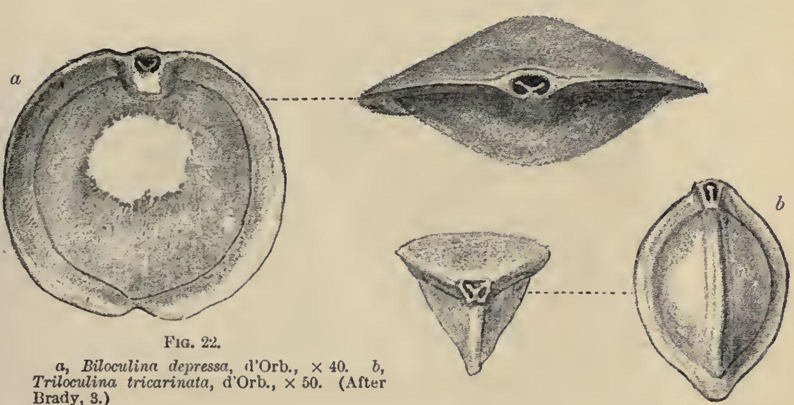

Fig. 22.

*a*, *Biloculina depressa*, d'Orb., × 40. *b*, *Triloculina tricarinata*, d'Orb., × 50. (After Brady, 3.)

In *Triloculina* and *Quinqueloculina*[1] the chambers are likewise disposed about an axis of construction, and their mouths open alternately in opposite directions, but the median plane of any chamber is not that of its predecessor, but directed at a definite angle to it. It is as though in a *Biloculina* test, while the plane in which the new chambers are formed remains constant, the

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[1] These genera are now usually included in the genus *Miliolina*, though Schlumberger is inclined to retain the old generic distinctions.

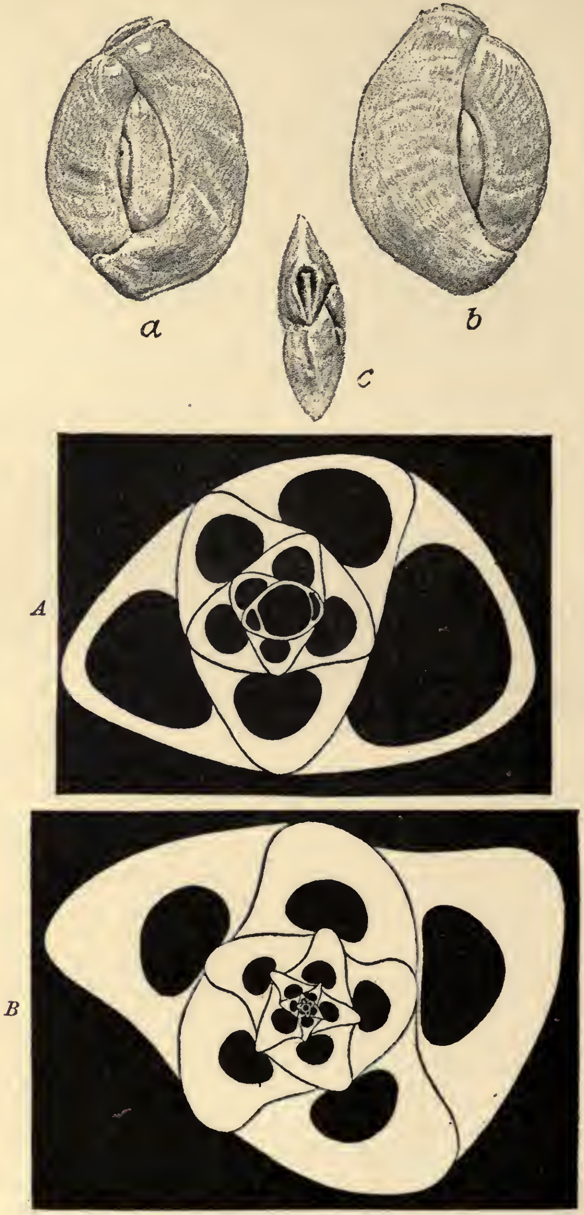

FIG. 23.

*Quinqueloculina seminulum*, Linn. *a-c*, views of test; *a*, *b*, from the sides; *c*, from apertural end. *A*, section of megalospheric, *B*, of microspheric form. *A* and *B* from Schlumberger (57). It will be noticed that *A* and *B* represent a less flattened form of test than that seen in *a-c*.

part of the test already formed were to rotate on its axis of construction through a definite angle in the interval between the formation of one chamber and the addition of its successor. In the genus *Triloculina* the rotation is through (approximately) one-third of the circumference, in *Quinqueloculina* through two-fifths, and the chambers are disposed in three and five radii respectively.

In these genera the width of the chambers is, moreover, less than in *Biloculina;* and in *Triloculina* three, in *Quinqueloculina* five chambers are exposed, at any given stage of growth on the contour of the test.

We may now turn to the phenomena of dimorphism as presented by members of this family.

In representatives of all the genera included in the list on p. 77, a well-marked difference has been shown to exist in the size of the central chamber in the two forms of the species. Thus in *Biloculina depressa* the diameter of the megalosphere ($M$)[1] has been found to vary from 200 to 400 $\mu$, and that of the microsphere ($m$)[1] from 18 to 25 $\mu$ (Fig. 24).

In *B. ringens* the contrast is not so great ($M = 54\ \mu$, $m = 20\ \mu$). In *Triloculina* $M = 204\ \mu$, $m = 18\ \mu$. In *Sigmoilina* $M = 96\text{-}150\ \mu$, $m = 27\text{-}36\ \mu$. In *Adelosina* $M = 90\text{-}330\ \mu$, $m = 18\ \mu$. In *Idalina* $M = 180\text{-}440\ \mu$, $m = 12\ \mu$. In *Massilina* a well-marked difference is said to be present, though the actual dimensions are not recorded.

Turning to the plan of growth, in *Cornuspira* and *Quinqueloculina* the tests are *uniform, i.e.* they are arranged on the same plan throughout, from the part which immediately succeeds the central chamber to the end of the test; and this is the case in both forms of the species. *Massilina* has biformed tests in both megalospheric and microspheric forms, the earlier chambers being arranged on the quinqueloculine plan, and the later on the spiroloculine. But in several of the other genera a marked contrast is found in the arrangement of the chambers in the megalospheric and microspheric forms. In the species of these genera the tests of the *megalospheric* forms are, for the most part, uniform, the arrangement characteristic of the genus being followed throughout the growth of the test, while the tests of the corresponding microspheric individuals are bi- or tri-formed, the plan of growth of the chambers changing once or twice before the test is complete.

Thus in many species of *Biloculina* the arrangement of the megalospheric form is biloculine throughout (Fig. 24, *a*). In the microspheric form (Fig. 24, *b*) the chambers succeeding the microsphere are arranged on the quinqueloculine plan, and this arrangement is maintained during the addition of a smaller or larger number of chambers, according to the species. At a certain stage the chambers become wider, and conform to the triloculine plan. Finally, the biloculine arrangement is assumed and maintained during the remainder of growth.

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[1] It will be convenient to use the letters $M$ and $m$ to indicate the diameters of the megalosphere and microsphere respectively, the "diameter" being taken to imply, when the central chamber is not spherical, the mean between the long and short diameters.

In like manner the megalospheric forms of *Triloculina* are built up on the triloculine plan throughout, while the microspheric forms begin life on the quinqueloculine plan, though they conform early to the triloculine (Fig. 25).

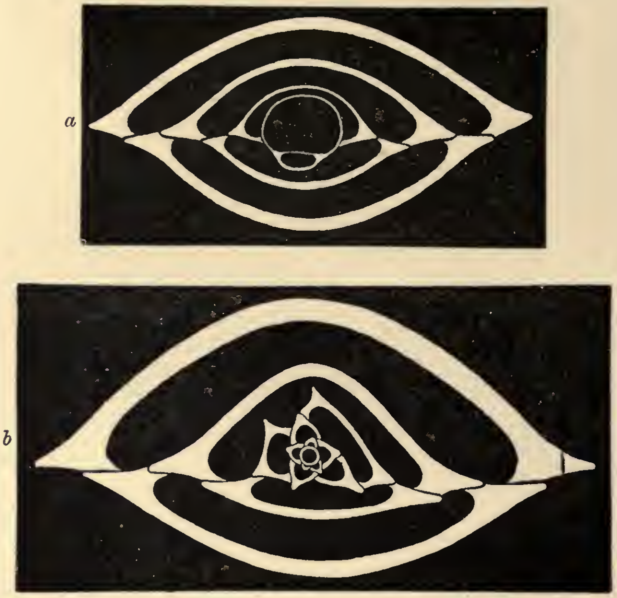

Fig. 24.

*Biloculina depressa*, d'Orb. Transverse sections. *a*, of the megalospheric form, × 50. *b*, of the microspheric form, × 90. (Two external chambers have been omitted in *b*.) (After Schlumberger, 55.)

I am indebted to the Cambridge Philosophical Society for permission to use the block from which these figures are prepared.

In some species it appears that a difference in the arrangement of the chambers is maintained throughout the growth of the test. Thus in *Biloculina lucernula*, Schwager, the microspheric form, commencing on the quinqueloculine plan, becomes triloculine, but appears never, according to Schlumberger, to attain to the biloculine arrangement, which the megalospheric form follows throughout. The two forms are shown to belong to the same species by similarities in the shape of the chambers, and also by the presence of a thin sandy layer on the surface of the test, which none of the other species inhabiting the same locality possess (55).

A difference in the arrangement of the chambers throughout growth is also said to be found in *Adelosina polygonia*, Schlumb., but it is in part of a different character. In this species the chambers are all arranged in a single plane in the megalospheric form, and after a preliminary quinqueloculine phase they are arranged in a single plane in the microspheric form. So far the arrangement agrees with that of *Biloculina*. But the chambers of *Adelosina polygonia* do not occupy a half turn of the spiral, as do the chambers in that genus, but only one-third or a quarter of a turn. In the microspheric form each chamber occupies one quarter of a turn of the spiral, and the tests are, in consequence, quadrangular in outline. In the megalospheric form the chambers occupy each one-third of a turn, and the resulting tests are triangular (Fig. 26). In about 1 per cent of the individuals of this form, however (310 were examined), the quadrangular arrangement was adopted in the last whorl (54).

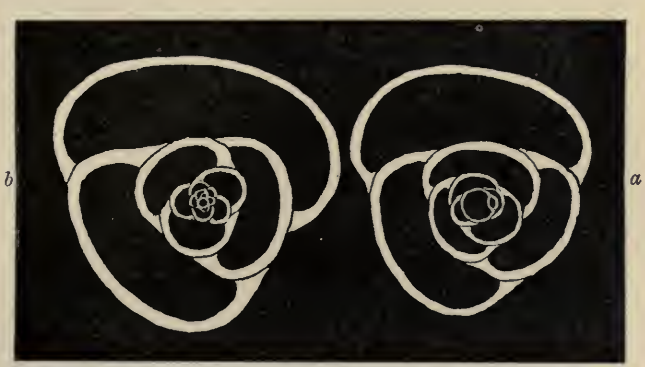

FIG. 25.

Sections of the test of *Triloculina schreiberiana*, d'Orb, × 66. *a*, the megalospheric form. *b*, the microspheric form. (After Schlumberger, 57.)

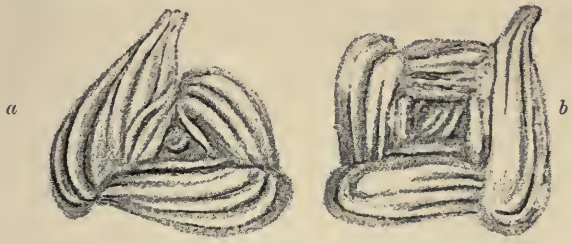

FIG. 26.

*Adelosina polygonia*. *a*, the megalospheric form; *b*, the microspheric form, × about 20 (After Schlumberger, 54.)

In the Miliolinidae, then, the tests of the megalospheric and microspheric forms of a species differ in the size of the central chambers, and also in some cases in the arrangement of the chambers which immediately succeed it. When this difference is found it depends on the fact that while the megalospheric form generally grows on a uniform plan throughout, the microspheric form assumes for a longer or shorter period of its growth an arrangement different from that to which it subsequently conforms, and one which is, in many cases, characteristic of another genus of the group.[1]

The term *Initial Polymorphism* was first applied by Munier-Chalmas and Schlumberger to a varying condition with respect to the arrangement of the initial chambers observed among different individuals of the megalospheric form of the fossil *Idalina antiqua*. It occurs also, as we shall see, in other genera.

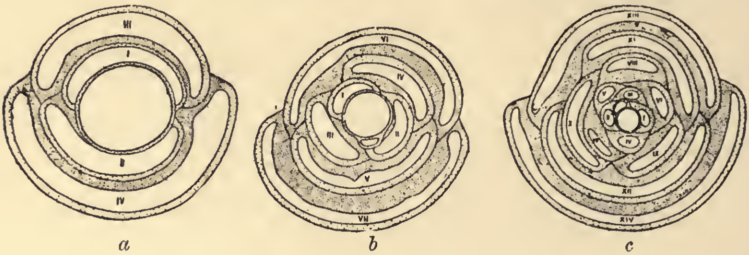

Fig. 27.

The central regions of transverse sections of three examples of the megalospheric form of *Idalina antiqua* (d'Orb.). Diameter of megalosphere in $a=440$, $b=400$, and $c=240\ \mu$. After Schlumberger. (It will be observed that the magnification of $a$ is greater than that of $b$ and $c$.)

In this species the megalospheric and microspheric forms are sharply contrasted in the size of their central chambers ($M=180-440\ \mu$, $m=12\ \mu$), and the arrangement of the chambers is, in the main, that characteristic of *Biloculina*. The microspheric form passes through quinqueloculine and triloculine stages to a biloculine condition, which, however, is converted in this genus in the later stages of growth to a uniloculine state, by the lateral extension of each of the chambers in turn, to embrace the whole of the previously formed test. The megalospheric form begins in many cases (Fig. 27, *a*), on the biloculine plan, to become unilocular at a later stage, like the microspheric form. In some cases, however, the initial chambers of this form are arranged on the triloculine plan (*b*), and in others again on the quinqueloculine (*c*), though the biloculine arrangement is soon assumed, in the latter case with a brief intermediate triloculine phase. Moreover, and it is important to notice this point, the forms with the largest megalospheres are those which assume the biloculine condition directly; those with the smaller megalospheres repeating the triloculine or the quinqueloculine arrangement.

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[1] I am not, however, aware of any definite form which the microspheric tests of *Adelosina polygonia* resemble.

Family *Hauerinidae.*—The biformed genera brought together in this family are said to be characterised by the cornuspira-like or milioline (tri- or quinque-loculine) arrangement of the chambers in the early stages of growth. In some cases, however, as in *Articulina conico-articulata*, Batsch, two forms of a species occur, one beginning in a large globular chamber with a short spiral passage leading to the later chambers, which are disposed in rectilinear series (Fig. 28, *a*), the other with a group of milioline chambers at the beginning (Fig. 28, *b*). It appears probable that these represent the two forms of the species, comparable with those found elsewhere.

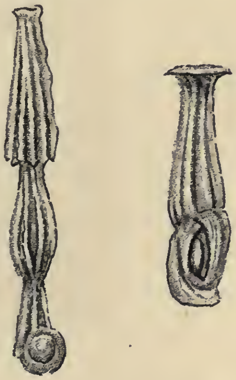

Fig. 28.

*Articulina conico-articulata*, Batsch. × about 55. *a*, from Millett (24, pt. ii.). *b*, from Brady (3).

Family *Peneroplididae.* — Four genera are here included — *Peneroplis*, *Orbiculina*, *Orbitolites*, and the fossil *Meandropsina*. As Carpenter pointed out, there is in this subfamily a well-marked series of forms with varying degrees of complexity of structure. Moreover, the contrast in the arrangement of the early chambers in the two forms of the species (that of the microspheric forms is here, I believe, described for the first time) appears to offer an instructive parallel to that met with in the Miliolinidae and elsewhere. Hence the group will be rather fully described.

*Peneroplis* is represented by a single species (*P. pertusus*, Forsk.) presenting, within certain limits, a remarkable range of variation.[1] In all cases the chambers are simple. During the earlier stages of growth they are disposed on a planospiral plan, and this may be followed until the test is complete, but more usually the terminal chambers are disposed in a rectilinear series. The width of the later chambers varies very much, as seen in the "crozier-shaped" and broad tests represented in Fig. 29.

Another varying feature is the "equitant" character of the chambers, as the result of which the earlier convolutions of the spiral part of the test are overlapped and hidden in varying degrees by the alar prolongations of the chambers which succeed them. The first few chambers communicate by single apertures, but the apertures soon become compound, consisting of a single or double row of pores, or, in the "dendritine" varieties, of an opening the margins of which are produced into branched and winding recesses.

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[1] Cp. for the superficial characters of the tests, Dreyer (13).

The extent of the septum which forms the terminal face of each chamber, and is perforated by the apertures, varies, of course, with the shape of the chambers, being small and more or less circular in outline in the crozier-shaped forms, and much elongated in the flattened forms. In the latter case it is markedly convex when seen from the side.

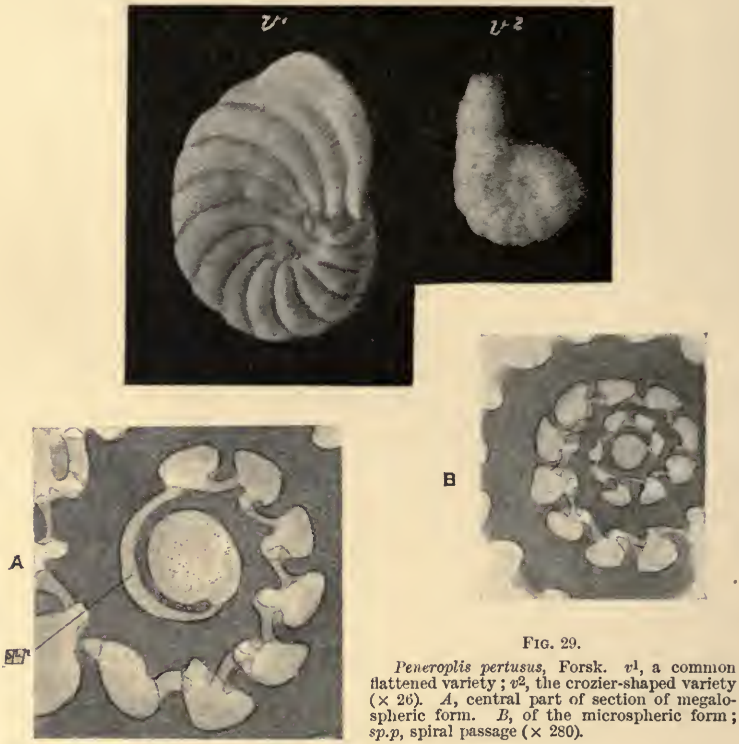

Fig. 29.

*Peneroplis pertusus*, Forsk. $v^1$, a common flattened variety; $v^2$, the crozier-shaped variety (× 26). *A*, central part of section of megalospheric form. *B*, of the microspheric form; *sp.p*, spiral passage (× 280).

In the *megalospheric form* the size of the oval megalosphere varies in samples from different localities. Thus, in 300 specimens from Aripo, on the coast of Ceylon, I find the average value of $M$ to be 30 $\mu$, and it varies in different individuals from 24-42 $\mu$. In a batch from Watson's Bay, Port Jackson, the average value is 42 $\mu$, and the individual variation ranges from 32-59 $\mu$. In two specimens in a West Indian gathering, however, $M = 19$ and 22 $\mu$.

A narrow *spiral passage* leads from the megalosphere and winds round half to three-quarters of its circumference before opening into the first of the spiral series of chambers. As Rhumbler has shown (35) the walls of the central chamber and the beginning of the spiral passage are traversed by minute radial perforations, so that the test formed in the earliest stage of the life of this form of *Peneroplis* is perforated, though the walls formed subsequently are, at any rate usually, imperforate, in accordance with the rule in the Miliolidea.[1]

The *microspheric* form of *Peneroplis* is very scarce in the material which I have examined. Among 1000 specimens I have met with only five. Its proportion to the megalospheric form appears, however, to vary in different localities. Thus, in a sample of sand from the Maldive Islands, dredged in 47 fathoms by Mr. J. S. Gardiner, the proportion is 3 to 108, or 1 to 36, which is about the same as obtains in *Polystomella*. On the other hand, in a batch of 480 specimens from Watson's Bay, I failed to meet with a single microspheric form. The values of $m$ in my specimens are 17, 18, 19, 22, and 24 $\mu$. On comparing these with the values of $M$, it will be seen that the megalosphere may, in some cases, fall below the microsphere in size. The two forms are, however, sharply separated by the fact that, as in *Orbiculina* and *Orbitolites*, the spiral passage is absent in the microspheric form (Fig. 29).

*Orbiculina.*—All the forms of the genus are included in a single species, *O. adunca* (F. and M.). Its distinctive features are the subdivision of the chambers into chamberlets, and the equitant character of the chambers in the earlier convolutions, giving rise to a prominent umbo at the centre of the flattened test. It affords a good example of the mode of occurrence of variation in one of the *Foraminifera* with a definitely symmetrical test.

Although the tests present themselves under a great diversity of external shape, the variations from the normal are limited to certain well-marked and definite lines. Fig. 30 shows the main varieties, as they are represented in a sample of ballast sand from the West Indies, kindly sent to me by Mr. F. W. Millett.

The youngest tests are uniformly nautiloid (Fig. 30, *a* and *b*), the chambers succeeding one another in a closely wound spiral. As the sections represented in Fig. 31 show, the chambers are elongated transversely to the course of the spiral; hence we may speak of their two ends as *inner* and *outer*—the former directed towards the concave side of the spire, the latter towards the convex side. While they are simple at their outer ends, the chambers of young specimens of all varieties are equitant at their inner ends, being produced on either side over the surface of the already formed test, in alar prolongations (cp. Fig. 32).

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[1] The tests of *Peneroplis* present throughout their growth a surface pitting, which is usually shallow, but may be so deep as to amount very nearly to perforation. Indeed I am not convinced that some forms are not completely perforated in the later as well as in the initial chambers. As we shall see below, the central chamber and spiral passage of the megalospheric form are perforated also in *Orbiculina* and *Orbitolites marginalis*. There appears therefore to be no justification for the separation of *Peneroplis* from the other genera of this family, as proposed by Rhumbler, on account of its supposed peculiarity in this respect.

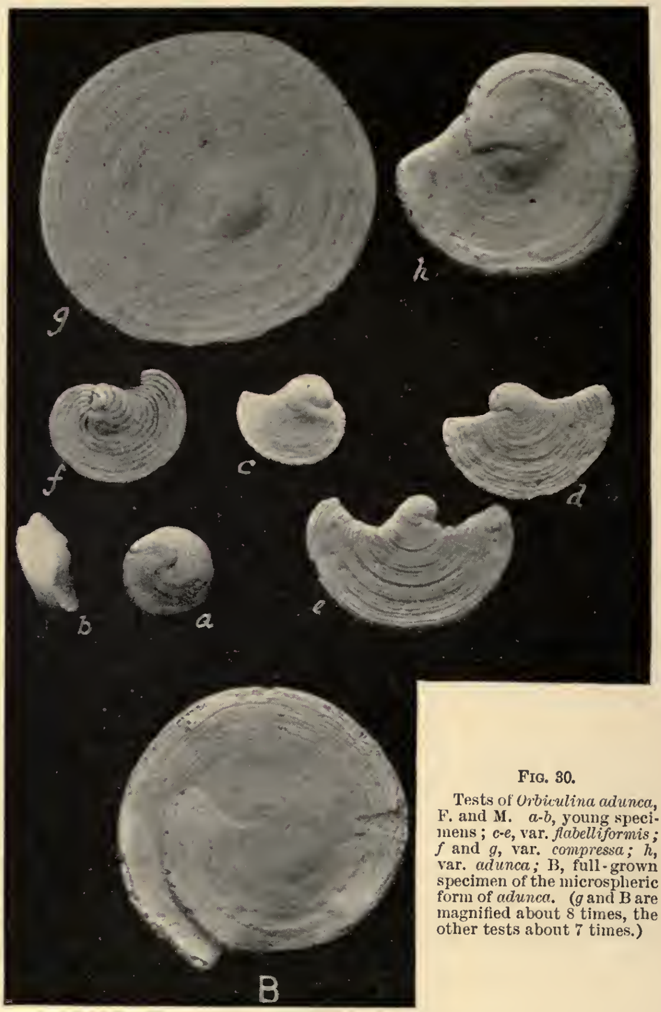

FIG. 30.

Tests of *Orbiculina adunca*, F. and M. *a-b*, young specimens; *c-e*, var. *flabelliformis*; *f* and *g*, var. *compressa*; *h*, var. *adunca*; B, full-grown specimen of the microspheric form of *adunca*. (*g* and B are magnified about 8 times, the other tests about 7 times.)

As growth proceeds, the chambers become more and more elongated, and the characters of the three main varieties become apparent, the shape ultimately assumed depending on the extent to which the successive chambers overlap their predecessors at either end.

In one variety, which may be called *flabelliformis*[1] (Fig. 30, *d* and *e*), the mode of growth changes from the spiral to the rectilinear. After the nautiloid stage the chambers lose their equitant character, and a series of long chambers is formed, each of which slightly exceeds its predecessor at either end. The fan-shaped tests here figured are thus produced.[2] They attain 2 mm. in their greatest diameter.

The commonest variety may be called variety *adunca* proper (Fig. 30, *h*). It includes the forms *O. adunca* and *O. orbiculus* (F. and M. spp.), of which the latter is the young stage of the former. Here the spiral mode of growth and the equitant character of the inner ends of the chambers are maintained until the test is complete. At their outer ends the chambers extend little, if at all, beyond the outer ends of their predecessors, and thus build up the abrupt prominence in the outline of the test, characteristic of this variety.

The third main variety is *compressa* (the *O. compressa* of d'Orbigny). In it the chambers cease to be equitant, and increase rapidly in length at both ends, being applied to and encircling more and more of the margin of the previously formed test. It thus comes about that the two ends of the chambers meet, forming a complete annulus. Henceforth the mode of growth is continued on the annular plan, and the disc-shaped tests represented in Fig. 30, *g*, are produced. In the sample examined the great majority of the specimens of *Orbiculina* are of the variety *adunca*. The next commonest variety is *compressa*, while *flabelliformis* is comparatively scarce.

This sample consisted in large part of the tests, young and old, of *Orbiculina*, and in hunting through it a form which did not fall into one or other of these varieties in some stage of growth, was very rare, the few exceptions being of an intermediate character.

The condition of the central chambers of *Orbiculina* can only be observed in sections.

Certain large forms of the variety *adunca* (Fig. 30, B), attaining a diameter of 6 mm., and distinguished also by the greater thickness of the tests and the much extended alar prolongations of the chambers, are shown by section to be *microspheric*, though in their younger stages the microspheric forms are not readily distinguished by external characters. In a set of 38 examples of this variety, of such a size that the microspheric forms were not externally differentiated, 34 were found, by section, to be megalospheric and 4 microspheric, a proportion of 1 to 9·5. The diameter attained by the megalospheric form of this variety is, in my examples, 4 mm.

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[1] In the description of Brady's figures of *Orbiculina* the term *flabelliform* is applied to two varieties—one (Fig. 7) the var. *adunca;* the other (Fig. 8) an exceptional form intermediate between varieties *adunca* and *compressa*. The term naturally, however, implies a bilaterally symmetrical test, and I have therefore used it as stated above.

[2] The cornucopia-shaped test, represented in Plate XIV. Fig. 4 of Brady's "*Challenger*" *Report*, is a rare form of this variety in which the increase is still less.

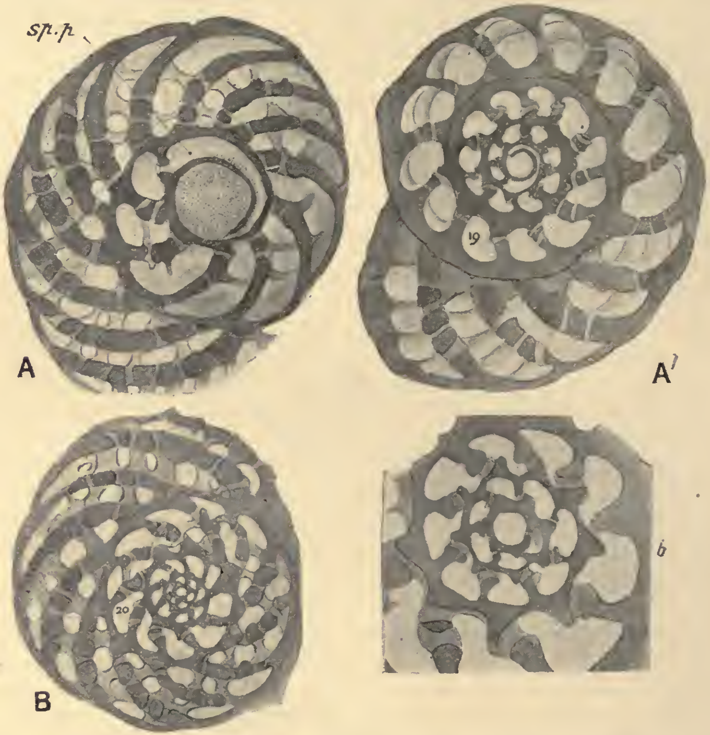

Fig. 31.

Central regions of sections of *Orbiculina adunca* in the median plane. A, large, A', small example of the megalospheric form. B, microspheric form, × 93. *b*, centre of B, × 250. *sp.p*, spiral passage.

I have failed to find a single microspheric form of the variety *compressa ;* 100 examples, examined in section, belong to the megalospheric form. Among 24 examples of the variety *flabelliformis*, however, one appears to be microspheric.

The diameters of the megalospheres in well-grown specimens of the varieties *adunca* and *compressa* are as follows :—

| | No. of Specimens examined. | Highest Value of $M$. | Lowest Value of $M$. | Average. |
|---|---|---|---|---|
| Var. *adunca* . . | 28 | 146 $\mu$ | 81 $\mu$ | 117 $\mu$ |
| ,, *compressa* . | 32 | 155 $\mu$ | 70 $\mu$ | 109 $\mu$ |

In *flabelliformis* the value of $M$ is less, though the average in my specimens is not below 64 $\mu$.

In the microspheric form the average value of $m$ in six cases is 18 $\mu$, the highest being 21 $\mu$, and the lowest 16 $\mu$.

In the *megalospheric* form the megalosphere is followed by a spiral passage reaching round $\frac{1}{2}$-$\frac{3}{4}$ of its circumference, and both megalosphere and spiral passage frequently exhibit the perforated condition found in *Peneroplis* (Figs. 31, A, and 32). The first of the spiral series of chambers is usually simple, but it frequently opens into its successor by two apertures, and in the second the transverse ribs generally make their appearance, which, becoming more marked in the following chambers, subdivide them into chamberlets. The chambers also communicate with one another by an increasing number of apertures, arranged in several rows along their peripheral walls.

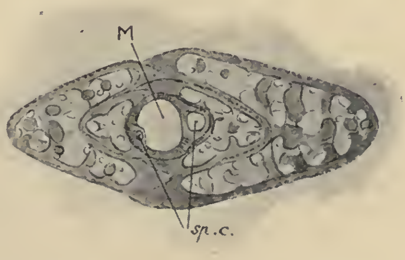

FIG. 32.

*Orbiculina adunca*, central part of a section of a megalospheric test passing transverse to the median plane. *M*, megalosphere; *sp.c*, spiral passage.

In the microspheric form of *Orbiculina*, as in that of *Peneroplis*, the microsphere opens direct into the first of the spiral series of chambers, and in this form there are generally some twenty simple chambers communicating by a single aperture before the subdivision into chamberlets begins (Fig. 31, B and *b*).

Such are the characters of well-grown specimens of *Orbiculina*; but on examining the construction of the tests of small specimens, as displayed in section, a mode of variation of a different kind becomes apparent, one which illustrates the phenomenon of Initial Polymorphism described by Munier-Chalmas and Schlumberger in *Idalina*. In the sample of sand which furnished the varieties above described were numbers of small megalospheric specimens resembling the young of the typical forms (*c* and *f* in Fig. 30), but beginning in a megalosphere of small size. In the specimen represented in Fig. 31, A′, the central part of one of these is seen in section. Here the megalosphere measures only 34 $\mu$ in diameter. Associated with the small size of the megalosphere of these forms is a long series of single chambers before the subdivision into chamberlets begins. In both characters they thus vary in the direction of the microspheric form, though always distinguishable from it by the presence of the spiral passage. In *Orbiculina* then, as in *Idalina*, the construction of the early part of the test is correlated with the size of the megalosphere. If it is small the arrangement approaches that of the microspheric form, if large it departs more widely from it.

Another feature met with in some of these stunted forms, though by no means in all, is that the subdivision into chamberlets may be incomplete or wholly absent. Sometimes the subdivision dies out in the terminal chambers after becoming established in their predecessors; in others it is absent throughout the test. I am inclined to regard these latter forms as examples of *Orbiculina* which have lost their secondary septation by "degeneration" rather than as representatives of *Peneroplis*, because of the existence of the intermediate forms just alluded to, in which the subdivision dies out in the terminal chambers, and also because they agree so closely in external features with small examples of "typical" *Orbiculina*, that they cannot be distinguished from them by the external characters of the tests.[1]

Four well-marked species are generally included in the genus *Orbitolites*, of which three—*O. marginalis*, *duplex*, and *complanata*—are intimately related to one another, and form a remarkably complete series of grades of development, while *O. tenuissima* stands apart. The three former are inhabitants of the littoral zone of tropical and subtropical seas, while the last lives in the deeper parts (250-1700 fathoms) of the North Atlantic, from which it extends into the Mediterranean.

In all the annular arrangement of the chambers is assumed early in life, the tests have a flattened discoidal shape, and an umbo is absent, as the chambers are not equitant at any stage of growth. All but the earliest chambers are subdivided into chamberlets.

In *O. marginalis* (Lamk.) the chamberlets are generally somewhat quadrangular when seen on the face of the disc, and the chambers they compose have an evenly curved outline. The disc consists of a single layer of chambers, and they are throughout simply applied to the peripheral margins of their predecessors. The radial septa which divide the adjacent chamberlets of an annulus from one another are traversed at their peripheral border by a canal, which places the chamberlets in communication with one another, and the canals of any one annulus may thus be regarded (following Carpenter's nomenclature) as composing an *annular canal*. From the canal, as it traverses a septum, a passage leads in a radial direction and opens either to the exterior by a pore at the margin of the disc, or into a chamber of the succeeding annulus, as the case may be. In this species the canals all lie in one plane, which is the median plane of the disc (cp. Fig. 38, *m*).

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[1] I have not had the opportunity of examining examples of *Archiacina*, but from the figure given by Schlumberger (50, Plate III. Fig. 2) it seems possible that this may be a form of variety *compressa* which has similarly lost the subdivision of its chambers.

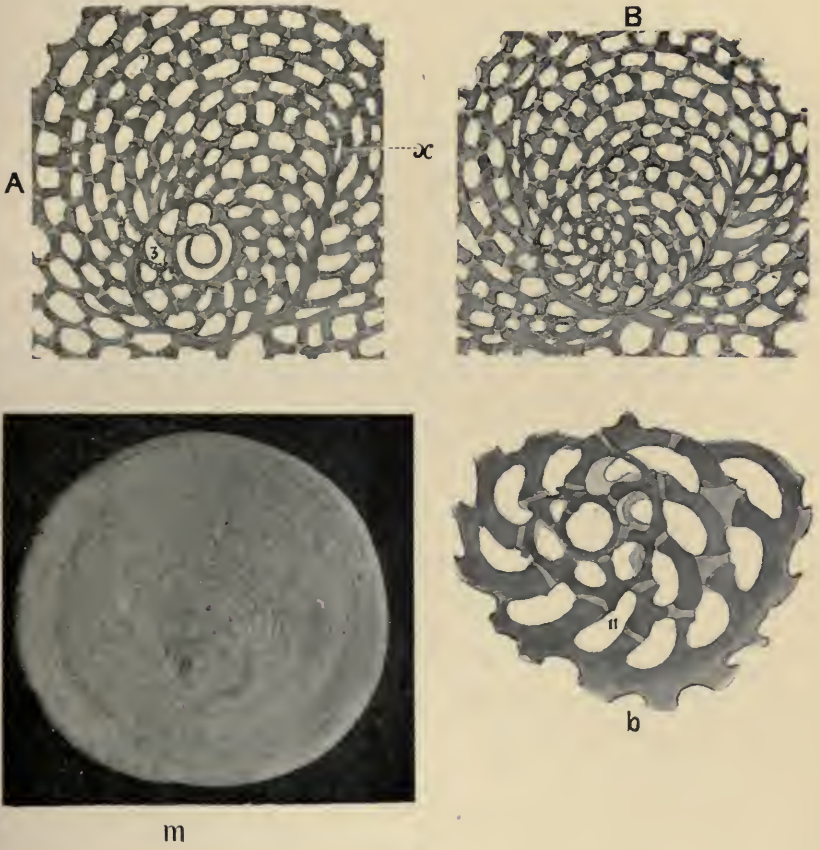

Fig. 33.

*Orbitolites marginalis*, Lamk. m, whole test (× 20); A, centre of megalospheric, B, of microspheric form, × 100; b, centre of latter, × 280; $x$, the outer end of the last series of chamberlets which follows the spiral mode of growth. The figures 3 and 11 in A and *b* mark the last of the undivided chambers in the two forms respectively.

The *microspheric* form (Fig. 33, B and b).—The microsphere opens directly, without the interposition of a spiral passage (as appears always to be the case in the Peneroplididae), into the first chamber. The chambers are arranged at first in a gradually expanding spiral, eleven to sixteen simple chambers succeeding one another as in the genus *Peneroplis*, but communicating by single apertures. As the spiral increases in width the chambers become divided into chamberlets, and the number of apertures is correspondingly increased, the arrangement at this stage repeating that which in the earlier stages of growth is common to all varieties of *Orbiculina*, except that there are no alar prolongations. When the stage of the spiral mode of growth is complete, the chambers become successively more and more embracing and the annular arrangement is attained.

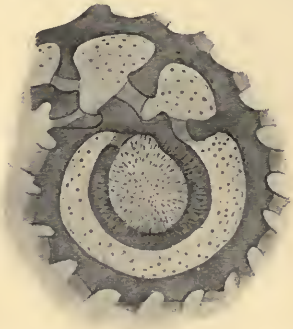

Fig. 34.
Central chambers of *O. marginalis*, showing the perforated wall of the megalosphere.

In the *megalospheric* form (Figs. 33, A, and 34) the megalosphere is pear-shaped. A spiral passage leads from it, and extends round about three-quarters of the circumference of the megalosphere. As in the case of *Peneroplis* and *Orbiculina* the walls of the megalosphere and the spiral passage may be perforated (Fig. 34). The single chambers which follow are usually only three or four in number, and beyond, the chambers become subdivided, and the arrangement resembles that of the microspheric form.

The dimensions of the central chambers in the specimens which I have examined are as follows. It will be seen that as in *Peneroplis* those of the megalosphere vary in the samples from different localities.

| | No. of Specimens examined. | Highest Value of $M$ or $m$. | Lowest Value of $M$ or $m$. | Average Value of $M$ or $m$. |
|---|---|---|---|---|
| Megalospheric— | | | | |
| from Aripo (Ceylon) . | 43 | 53 $\mu$ | 24 $\mu$ | 36 $\mu$ |
| ,, W. Indies . | 47 | 78 $\mu$ | 37 $\mu$ | 51 $\mu$ |
| Microspheric— | | | | |
| from Aripo . . | 17 | 19 $\mu$ | 15 $\mu$ | 17 $\mu$ |
| ,, W. Indies . | 1 | ... | ... | 18 $\mu$ |

In *Orbitolites duplex*, Carpenter, the arrangement is at first sight similar, but the chamberlets are more elongated in a direction perpendicular to the face of the disc. Here, again, they are in communication by a single annular canal, but the apertures which open out of it and lead to the chamberlets of the succeeding annulus are disposed obliquely and lie in two planes, one on either side of the median plane (cp. Fig. 38, *d*). There are thus in typical specimens two rows of pores at the margin of the disc. There is, moreover, a difference in the shape and arrangement of the chamberlets. Instead of the regularly curved series of quadrangular chamberlets which make up the well-marked annuli of *O. marginalis*, the chambers (especially those near the centre of the test) are oval, being elongated in a tangential direction, and fall into lines like those on the back of a watch, making what is known as the "engine turned" pattern.

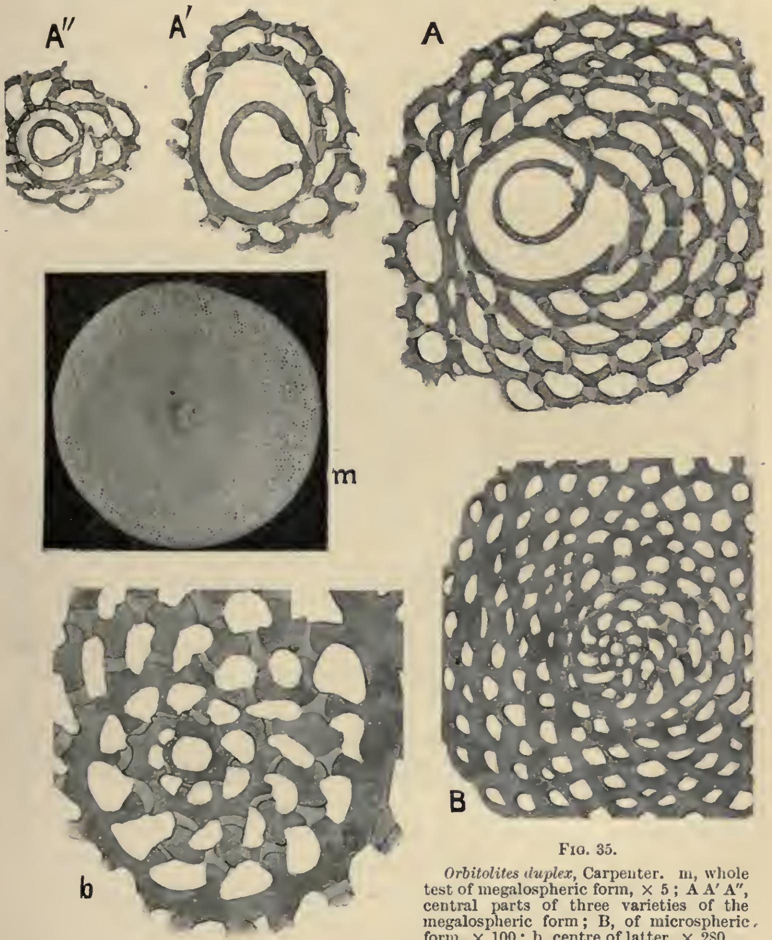

Fig. 35.

*Orbitolites duplex*, Carpenter. m, whole test of megalospheric form, × 5; A A' A'', central parts of three varieties of the megalospheric form; B, of microspheric form, × 100; b, centre of latter, × 280.

In an example of the *microspheric* form the microsphere is 20 $\mu$ in diameter, and here again the spiral canal is absent (Fig. 35, B and b). There are eleven single chambers before the subdivision into chamberlets begins, and then the orbiculine arrangement is assumed, to pass in turn into the annular, as in *O. marginalis.*

In the *megalospheric* form the megalosphere is round or pear-shaped, and has an average mean diameter of about 76 $\mu$ (the diameters in 108 specimens vary between 49 and 110 $\mu$). The spiral passage almost encircles the megalosphere, and is wider than in *O. marginalis.* Though it sometimes communicates with only a single chamber (Fig. 35, A″), there are usually two to five chamberlets into which it opens directly, by as many apertures (Fig. 35, A and A′), so that the peneropline and orbiculine stages are in such cases abridged, and the annular arrangement speedily attained.

In a sample of the tests of *O. duplex* from Aripo, all (108 in number) were megalospheric. The specimen of the microspheric form above described is from Funafuti in the Pacific.

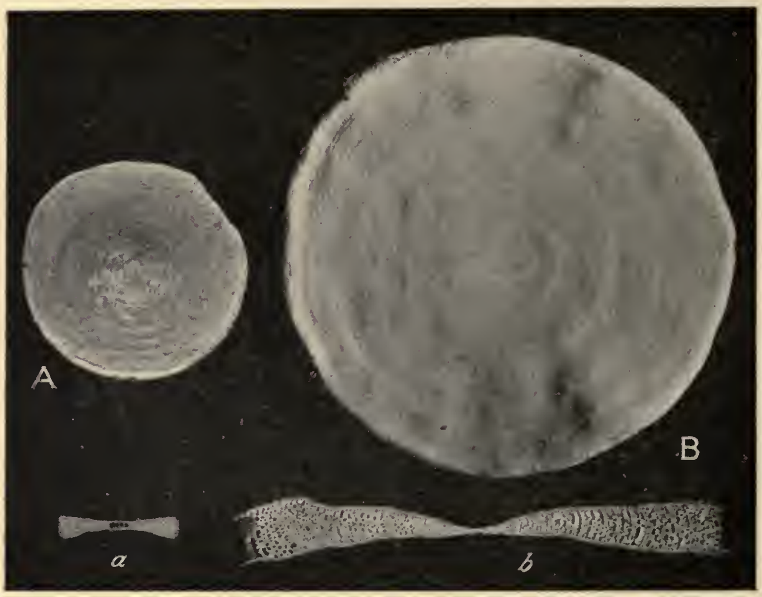

FIG. 36.

*Orbitolites complanata*, Lamk. The megalospheric (A, *a*) and microspheric (B, *b*) forms, whole, and in section, × 5. The primitive disc is seen at the centre of A and *a*, and young megalospheric individuals (= primitive discs) may be seen at the left-hand end of *b*.

In *Orbitolites complanata*, Lamk. (cp. p. 73), a much greater degree of complexity is attained, in that the chambers, which in *O. duplex* are elongated in a vertical direction, are differentiated into three several layers—two layers of *superficial chamberlets*, one on either face of the test, and an *intermediate* layer of columnar spaces lying between them (Figs. 36, *b*, and 38, *c*). There are here two annular canals corresponding to each annulus of chamberlets, lying at either end of the columnar spaces in the two strata of the test between these and the superficial chamberlets. There are abundant communications between the chamberlets, and those at the periphery open to the exterior by vertical rows of pores at the margin of the disc.[1]

*The Microspheric Form.*—The centre of the disc of this form is much thinner than that of the megalospheric (Fig. 36, *a* and *b*). It is often the seat of secondary growth which occurs towards the end of the vegetative phase, giving rise to a button-like excrescence and accompanied by absorption of the original central chambers. If this has not occurred an arrangement similar to that of the central regions of the microspheric forms of *marginalis* and *duplex* is revealed by section. In two specimens I find that the microsphere has a mean diameter of 17 and 18 $\mu$, a spiral passage is absent, and seven to eleven single chambers succeed the microsphere. These are followed by subdivided chambers, continuing the spiral, and the mode of growth then changes to the cyclical as in the other species (Fig. 37, B).

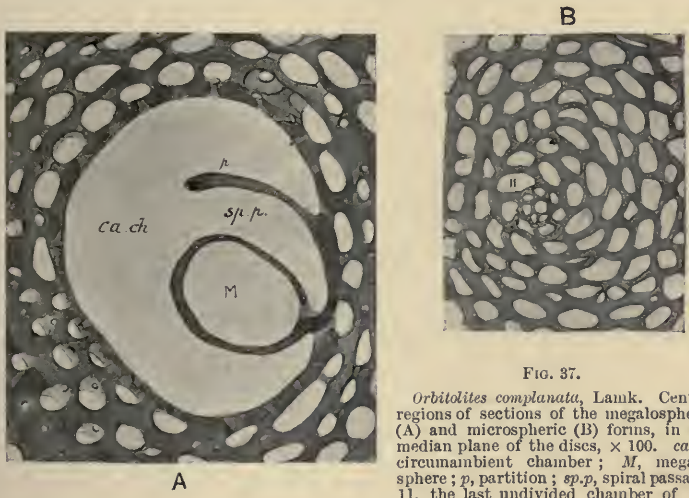

Fig. 37.

*Orbitolites complanata*, Lamk. Central regions of sections of the megalospheric (A) and microspheric (B) forms, in the median plane of the discs, × 100. *ca.ch*, circumambient chamber; *M*, megalosphere; *p*, partition; *sp.p*, spiral passage; 11, the last undivided chamber of the microspheric form.

In some varieties, at least, of this species the microspheric form attains a much larger size than the megalospheric (Fig. 36, A and B), and the large forms with double and contorted margins, described as variety *laciniata*, Brady, are all, as far as my experience goes, microspheric. It seems, indeed, that the peculiarity of the margin of this form may be regarded as a provision for supplying a larger number of peripheral brood chambers for the accommodation of the megalospheric young into which the protoplasm becomes divided.

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[1] For the details of the structure, cp. Carpenter's descriptions (8 and 9).

The *megalospheric* form begins in a structure called by Carpenter the *primitive disc* (Figs. 36, 37, A, and 38). It consists of (1) the megalosphere, which is pear-shaped (about 107 $\mu$ in mean diameter); (2) a spiral passage leading from the megalosphere, and opening into (3) a large crescent-shaped chamber, one horn of which extends round one side of the megalosphere, and the other along the outer side of the spiral passage. It results from this arrangement that the outer wall of the latter forms a partition (*p*) disposed perpendicularly to the flattened surface of the primitive disc, and separating the spiral passage from the crescentic chamber. The partition ends in a free border. The spiral passage with the crescentic chamber together compose the *circumambient chamber* of Carpenter. The whole of the peripheral wall of the circumambient chamber is perforated by pores opening into the innermost chamberlets, which are thus disposed in a complete annulus from the beginning. In some primitive discs there is a single row of pores at the margin, in others there are two or three rows. In the latter case the three-layered arrangement of chamberlets characteristic of *O. complanata* is assumed directly; while in the former the region of the test immediately surrounding the primitive disc may present varying degrees of development. In some (Fig. 38) the rings of chamberlets are at first in single series, arranged on the *marginalis* type, and they are succeeded by annuli on the *duplex* type, the three-layered character being ultimately assumed. In others the arrangement begins on the *duplex* type. Here, again, we have examples of *initial polymorphism.*

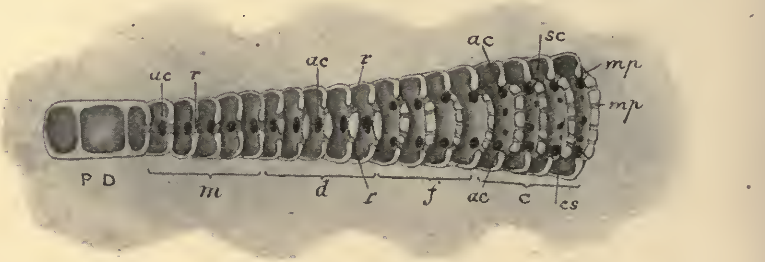

FIG. 38.

Diagram representing the transition from the simple ("marginalis") to the complex ("complanata") type of structure in the growth of a sub-typical individual of *Orbitolites complanata.* The primitive disc and half the test of a megalospheric form are represented in section. The letters P D are placed beneath the centre of the primitive disc. *m*, part of test formed on the *marginalis* type; *d*, that formed on the *duplex* type; *f*, that formed on the type of a fossil form of *O. complanata; c*, that of the typical *O. complanata; ac*, annular canals; *cs*, columnar spaces; *mp*, marginal pores; *r*, radial canals; *sc*, superficial chamberlets. (After Carpenter, but modified.)

On comparing the primitive disc of *O. complanata* with the centre of the tests of the megalospheric forms of the other species, it appears that the crescent-shaped chamber of *complanata* may be regarded as an expansion of the end of the spiral passage. In those forms of *duplex* in which the spiral passage communicates with more than one chamberlet the end is somewhat expanded. An extension of this expansion round the outer side of the spiral passage would give rise to the complete crescentic chamber which we find in *complanata*.[1]

Looking back on the series of forms of Peneroplididae hitherto examined, a gradual increase in complexity of structure is to be observed. We pass from *Peneroplis*, with undivided chambers disposed at first on a spiral and often, later, on a rectilinear plan, to *Orbiculina*, with subdivided chambers similarly disposed, though in one variety of the megalospheric form the annular arrangement is assumed. In *Orbitolites marginalis* the chambers and pores are disposed in a single plane, and in the early stages of growth we find arrangements repeating in some of their features those of *Peneroplis* and *Orbiculina* before the annular arrangement which is characteristic of *Orbitolites* is arrived at. *O. duplex*, with its double series of pores, furnishes an intermediate stage to the complex three-layered condition of *O. complanata*.

In his Report on the genus *Orbitolites*, Carpenter made this series of genera and species the subject of a "Study of the Theory of Descent," and laid stress on the remarkable manner in which the forms of the simpler members are repeated in the life-history of the more complex. When this Report was published (1883) attention had only recently been drawn to the phenomenon of dimorphism in the Foraminifera, and Carpenter does not appear to have been aware of the existence of the microspheric forms, as constituting a distinct set of individuals.

On comparing the mode of growth of the microspheric and megalospheric forms, we find a contrast between them comparable to that presented by the Miliolinidae. While the microspheric forms repeat successively the shapes and arrangements of chambers which are permanent in other, and in this case, simpler, members of the group, in the megalospheric forms these stages are to a greater or less extent abridged or altogether omitted. Thus in the megalospheric form of *Orbitolites marginalis* the peneropline series of single chambers which succeeds the spiral canal is fewer in number than in the microspheric form, but the orbiculine arrangement is well represented. In this form of *O. duplex* the peneropline condition has almost or entirely disappeared, and the orbiculine stage is much abbreviated. In *O. complanata* both peneropline and orbiculine arrangements have entirely gone in the megalospheric form.

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[1] The remarkable fossil form *Meandropsina* described by Schlumberger (59) appears to be related to *Orbitolites*, the surface of the disc being covered with a layer of chamberlets arranged in a Meandrina-like manner. Schlumberger finds both microspheric and megalospheric forms are represented in his specimens.

We turn now to the other species, commonly included in the genus *Orbitolites*, the *O. tenuissima* of Carpenter (Figs. 39 and 40).

The tests are exceedingly thin ($\frac{1}{300}$ inch), though they may attain 30 mm. in diameter.

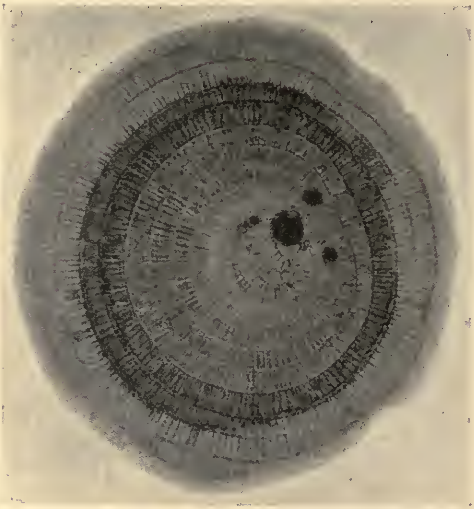

Fig. 39.

*Orbitolites tenuissima*, Carp. The complete test, × about 11, from a photograph.

There are undoubtedly points of similarity in structure between this species and *O. marginalis*, the simplest of the other members of the genus. The annular arrangement succeeds a spiral one, and the annuli are divided into chamberlets by septa disposed in a manner which is very similar to that found in *O. marginalis*, especially in examples from deep water in which the radial septa are sometimes incompletely developed. Coming to the middle of the test, however, we find ourselves in new country. In five specimens a globular central chamber about 31 $\mu$ in diameter[1] occupies the centre, and leading from this is a succession of narrow elongated chambers, wound in a planospiral manner about the central chamber in some 7-8 convolutions. The lengths of the several chambers vary from 2¼ convolutions to ⅓ of a convolution of the spiral. The arrangement and mode of communication of the chambers recalls the irregular spiroloculine tests of Ophthalmidium (Fig. 41). As the five specimens have an approximately similar arrangement, it is probable that the form we are dealing with is megalospheric, though the size of the megalosphere is small.

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[1] In that figured in Plate I. Fig. 1 of Carpenter's Report the central part of the test appears to have been left blank, without any intention of depicting a central chamber of the size of the blank space. The specimen here figured was obtained by the *Travailleur* in the Bay of Biscay, and I am indebted to the authorities of the British Museum for the opportunity of giving a photograph of it. The central chamber measures $30 \times 31$ $\mu$. In the four other specimens in which I have been able to obtain evidence of the size of the central chamber, it appears to be about the same.

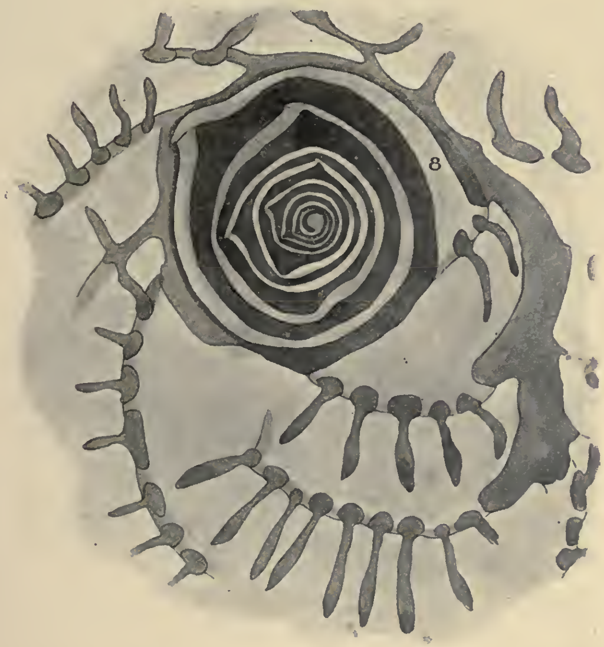

Fig. 40.

*Orbitolites tenuissima*, Carp. Central region of the specimen represented in Fig. 39. × 80. The figure 8 is in the eighth and last convolution of the inner series of chambers.

When comparing the central regions of *O. marginalis* (megalospheric) with those of *O. tenuissima*, Carpenter regarded the spiral passage of the former as representing "the whole of the original 'spiroloculine' coil, drawn up into itself" (p. 24). The difficulty, however, of recognising the long spiroloculine (or *Ophthalmidium*-like) coil of *tenuissima* in any of the modifications of the spiral passage met with in the other species of the genus *Orbitolites* is so great that we are led to doubt whether *tenuissima* is really allied to them. On the other hand, the resemblance of the inner chambers of *tenuissima* to *Ophthalmidium*, a member of the Hauerinidae, suggests that it may be derived from this family, and have acquired the cyclical mode of growth independently. The acceptance of this view is perhaps rendered easier by the existence of another group, the *Operculina-Cycloclypeus* series, in the higher members of which the annular mode of growth is likewise attained (see p. 128). It seems at any rate worth while to entertain the possibility of this explanation, before accepting a conclusion so damaging to a body of evidence which may be found, if duly considered, to furnish the clue to many complicated problems of relationship.[1]

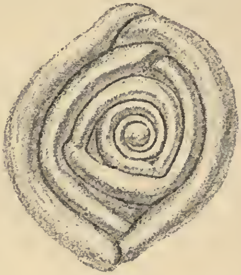

FIG. 41.

*Ophthalmidium tumidulum*, Brady. "*Challenger*" *Report*, Pl. XII. Fig. 6.

Family *Alveolinidae.*—The genus *Alveolina* which represents this family contains a number of recent and fossil forms which appear to branch off from the Miliolid stock in the neighbourhood of the genus *Orbiculina*. They are characterised by elongation of the chambers in a plane at right angles to that in which they are developed to form the disc-shaped tests of *Orbitolites*—that is, in the direction of the axis of the spire. The result is the formation of a series of oblate, spherical, ovoid (Fig. 42, b), fusiform, and cylindrical (Fig. 42, a) tests, each chamber extending beyond its predecessors laterally to a greater or less extent, and thus increasing the axial length of the test. The chambers are short in the direction of the plane of the spire, and subdivided into chamberlets by vertical septa lying parallel with that plane. In

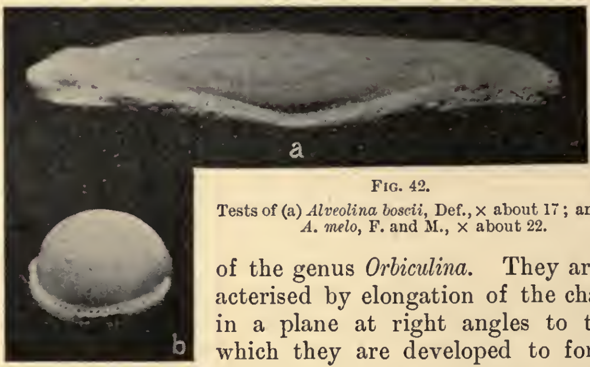

FIG. 42.

Tests of (a) *Alveolina boscii*, Def., × about 17; and (b) *A. melo*, F. and M., × about 22.

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[1] It would perhaps be premature, while we are not yet acquainted with the two forms of *tenuissima*, to alter its systematic position, but should this view of its relationship be confirmed, it must be separated as a distinct genus to which the name *Cyclophthalmidium* might be given.

the recent *Alveolina boscii* the chambers are further subdivided by horizontal septa.

Schlumberger states (51) that Munier-Chalmas has recognised the phenomenon of dimorphism in a fossil *Alveolina*, of which the microspheric form is distinguished by a very small central chamber surrounded by five simple chambers, which are not subdivided. It would appear, therefore, that a peneropline stage is represented also in the development of the microspheric form of this genus. In specimens of the megalospheric form of *A. boscii* I find the central chamber to be ovoid and to measure about 150 $\mu$ in long diameter.

### *Life-histories and nuclear characters of the Miliolidea.*

Direct observations on this head are very scanty.

In *Cornuspira*, as we have seen (p. 74), the megalospheric form may give rise to megalospheric young, and the same event has occurred in a specimen of a Milioline form (? *Quinqueloculina*) in my possession. In this case the megalosphere of the parent was only 30 $\mu$ in diameter, and those of the young varied from 20 to 43 $\mu$. Schlumberger (49) and Schaudinn (42) have also described the production of broods of young, which were evidently megalospheric, in the Miliolinidae (the latter author in *Quinqueloculina seminulum*, L.), but the nature of the parent is not indicated. In these Miliolinidae it appears that the division of the protoplasm to form the young may occur within the parent test or outside it.

The production of megalospheric young by the breaking up, within the test, of the protoplasm of a megalospheric parent, had occurred in a specimen of *Peneroplis* described by Schacko (39); and in this case the young, consisting of the central chamber and spiral passage, resemble in size and shape the corresponding parts of the parent. Bütschli (7) has found a single nucleus in two specimens of *Peneroplis*, and 18-20 in another. In all three cases the parents were megalospheric, and in the last we may suppose that the division of the nucleus had occurred preparatory apparently to the production of a brood of megalospheric young, as in the cases of *Discorbina* and *Patellina* (see p. 123).

Of the genus *Orbitolites* our knowledge is somewhat fuller.

I have a specimen of the megalospheric form of *O. marginalis* in which the two or three peripheral annuli contain young, consisting of the megalosphere and spiral passage. The chambers containing them are in this case not different from the ordinary marginal chambers.

A specimen described by Semper (63) appears to have belonged to *O. duplex*, and this also is a megalospheric parent with megalospheric young. He mentions that the chambers containing them were "ziemlich viel grösser" than those internal to them, and thus it may be the case that in this as in other characters *O. duplex* is intermediate between *marginalis* and *complanata.*

In *O. complanata* the microspheric forms known as var. *laciniata* produce megalospheric young. The double convoluted margins of this variety are not completely subdivided into chamberlets as are the more central regions of the disc, but, in part at least, contain spacious chambers extending through the thickness of the disc, and round a large part of the periphery. Into these (as well as into similar large chambers in the secondary growths formed on the surface of the disc) the protoplasm withdraws, at the reproductive phase, from the whole central region of the original test, and becomes divided up into young megalospheric forms, which are liberated by the breaking down of the limiting walls. This mode of reproduction in *O. complanata* was first described by Brady (4), though he was not aware of the full significance of his observation, and afterwards by myself (20). In Fig. 36, *b*, a form with a simple margin is seen bearing megalospheric young.

The megalospheric form of *O. complanata* may also, as we have seen (p. 74), give rise to a brood of young of the same nature, but there can be no doubt that a phase recurs in the cycle of the life-history in which, as in *Polystomella*, zoospores are produced.

The microspheric form of *O. complanata* has, scattered through its protoplasm, large numbers of rounded nuclei, which may frequently be found constricted as though in process of simple division. In the megalospheric form a large nucleus may often be found throughout the greater part of the life lying in the primitive disc, and thus, as already pointed out (p. 71), at the central part of the protoplasm (20).

*Calcituba polymorpha* appears to be a degenerate member of the Miliolid stock. Its life-history, as exhibited in aquaria, has been investigated by Schaudinn (46). It forms wide adherent expansions on the surface of foliaceous algae on which it feeds, spreading in irregular annular patches—like fairy rings. The colony may begin as a spherical central chamber with a spiral passage leading from it—the form which occurs so frequently at the centre of the megalospheric tests of the compact Miliolidea. From such a centre branching offsets extend in a radial direction over the algal substratum, and as this is disintegrated by the organism feeding on it, the central regions, left unsupported, may fall away, while the margins spread in the annular fashion described. The portions which so fall may start a similar colony forthwith, or their protoplasm may break up into small portions (1-20) of varying size, which at first crawl about as naked masses, and later, on initiating a new colony, may secrete the Miliolid form of test mentioned above.

The walls are chitinous tubes with a calcareous deposit. They are imperfectly divided into chambers, and are not perforated. A flagellate stage did not come under observation. The protoplasm contains large numbers of small nuclei.

### ORDER **Textularidea.**

This order contains a number of genera which are excellent examples of the multiform (biformed and triformed) condition of the test.

The arrangement which has been regarded as typical of the genus *Textularia* is one with two rows of alternating chambers, but Schubert has recently drawn attention to the fact (65) that many, if not all the forms included in it, are biformed, some having the earlier chambers arranged in a planospiral, others in a rotaloid, and others again in a triserial manner, before the characteristic biserial arrangement is assumed. Thus "*Textularia*" *sagittula*, Def., begins as Schubert states, and as I have also had occasion to observe, in a planospiral series of chambers, the arrangement being, in fact, that characteristic of the genus *Spiroplecta*. Out of a batch of 63 specimens of this species collected at Plymouth in the month of July, I found 57 to be megalospheric, and 6 microspheric, a proportion of 9 to 1.

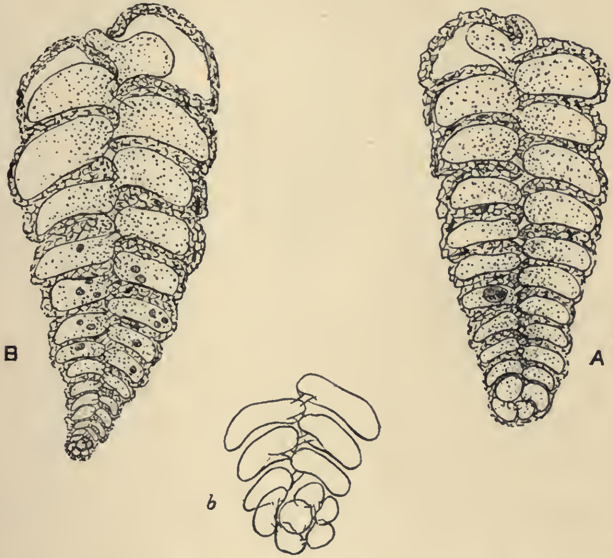

FIG. 43.

*Spiroplecta* (*Textularia*) *sagittula*, Def. A, the megalospheric, B, the microspheric form, × 55; *b*, the earlier chambers of the latter, × 150. A and B represent specimens stained, and mounted in Canada Balsam, and show the nuclei.

In the *microspheric* form (Fig. 43, B and b) $m = 15\text{-}18\ \mu$, and is followed by some five or six chambers arranged in a spiral before the alternating arrangement is assumed. One specimen contains at least 13 nuclei.

In the *megalospheric* form (Fig. 43, A), the average mean diameter of the megalosphere is about 60 $\mu$ (the limits of those measured were 44 and 72 $\mu$). The initial spiral is here somewhat shorter, consisting of four chambers. A single large nucleus is seen in these specimens some distance along the alternating set of chambers.

The spiral arrangement of the early chambers is much more conspicuous in *Spiroplecta annectens*, P. and J. (Fig. 44, A, B, and b).

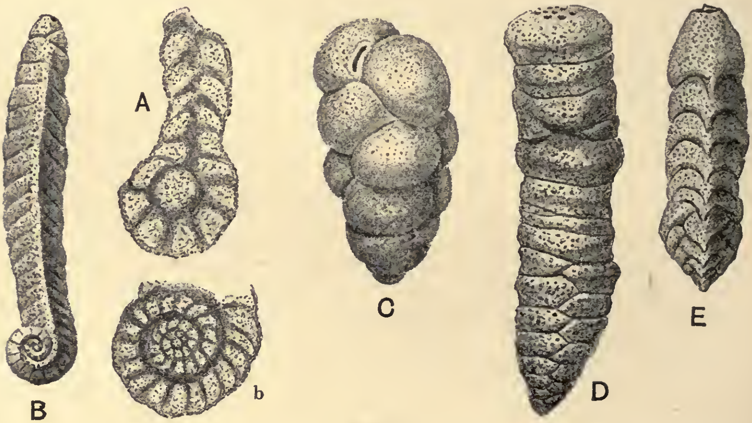

Fig. 44.

A, B, and b, *Spiroplecta annectens*, P. and J; A, the megalospheric, B, b, the microspheric form. C, *Verneuilina pygmaea*, Egger. D, *Bigenerina robusta*, Brady. E, *Clavulina angularis*, d'Orb. A and b, × 76, original; B-E, from Brady (3).

What appears to be the megalospheric form of this species has long been known as a Cretaceous fossil. The species occurs at the present day round the coasts of Australia, and has been recognised in sand from the Malay Archipelago by Mr. F. W. Millett (24, Part VII., 1900), to whom I am indebted for calling my attention to the evidence of dimorphism in this species, and for the opportunity of examining the specimens from which the following details are given.

Among six specimens of the *megalospheric* form (Fig. 44, A), the average value of $M = 60\ \mu$ (the limits of variation are 53 and 71 $\mu$), and one nearly complete spiral whorl of chambers intervenes before the straight and biserial part of the test begins.

The *microspheric* form attains a larger size. Among 15 specimens, the average value of $m = 17\ \mu$ (the limits being 11 and 20 $\mu$), and $2\frac{1}{2}$-$3\frac{3}{4}$ whorls of chambers arranged in a spiral form the earlier part of the test. The later, straight part is much longer than in the megalospheric form, and in both forms the biserial arrangement may give place to a uniserial one at the end.

The characters of other genera of this family are indicated in the table of classification, and some of them are represented in Fig. 44, C-E, and Fig. 54.

### ORDER **Chilostomellidea.**

I am not aware of any record of dimorphism in this order.

### ORDER **Lagenidea.**

Schlumberger has found representatives of both generations in *Nodosaria* (*Dentalina*) *guttifera* and *Nodosaria hispida*, the megalospheric forms beginning in a large initial chamber (Fig. 45, A), larger than that which succeeds it, and having only five or six chambers in all; the microspheric having a larger number of chambers, and tapering gradually to a fine point at which the little microsphere is situated. In such tests the phenomenon of dimorphism is presented in the simplest possible form.

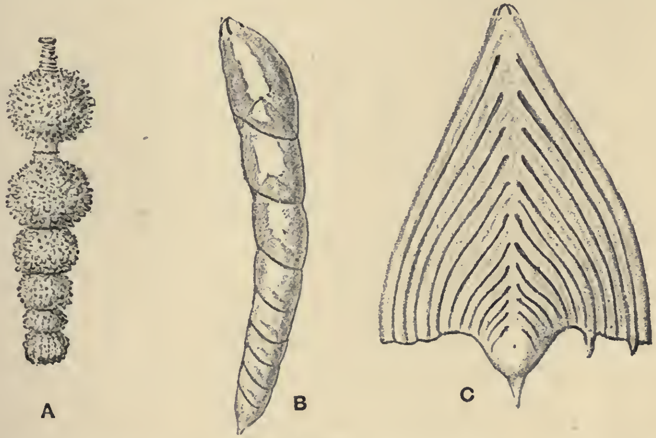

FIG. 45.

Megalospheric forms of—A, *Nodosaria hispida*, d'Orb. B, *Nodosaria* (*Dentalina*) *communis*, d'Orb. C, *Frondicularia alata*, d'Orb. (After Brady, 3.)

Fornasini (15) has shown that *Frondicularia* (Fig. 45, C) is dimorphic.

The monothalamous Lagenidae often present a great resemblance to the single chambers of *Nodosaria*, but the nature of the relation between the two groups is obscure. Neumayr derives the former from the latter by degeneration; Rhumbler, by the falling apart of the chambers. A remarkable feature of some Lagenidae is the "entosolenian" condition in which the tubular neck is, as it were, inverted into the interior of the test (Fig. 46, *b*). A similar inverted neck is found in *Cymbalopora*, and occasionally in *Polymorphina* (3, pp. 558 and 638).

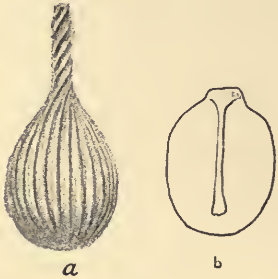

FIG. 46.

*a*, *Lagena sulcata*, W. and J., × 60. *b*, *L. globosa*, Montagu, showing the entosolenian neck. (After Brady.) × 80.

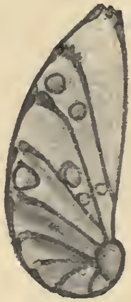

FIG. 47.

*Cristellaria crepidula*, F. and M., after Brady (3, Pl. 68, Fig. 1), showing the production of a brood of megalospheric young, of varying size, by a megalospheric parent. × 38.

The observations of Burrows and Holland (5) on *Cristellaria gibba*, and *C. platypleura* appear to show (though no measurements are given) that the authors have found dimorphic forms of *Cristellaria*. In *C. cenomana*, Schacko (40) describes a form which, he suggests, is microspheric, having a central chamber measuring 40 μ, while $M = 75$ μ. In the specimen of *C. crepidula* shown in Fig. 47, however, the size of the young chambers (which we may suppose to be megalospheres) varies much, and the smallest appear to measure about 40 μ in diameter; and as this measurement is rather large for the size of a microsphere, the microspheric character of Schacko's specimen is, at least, open to doubt.

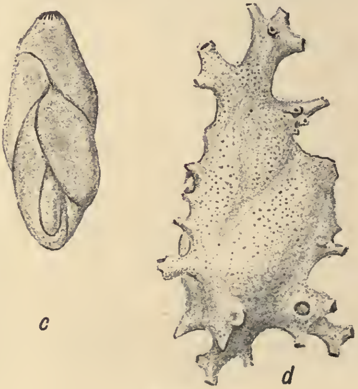

FIG. 48.

*Polymorphina compressa*, d'Orb.; *c*, the simple form, × 32; *d*, the fistulose form, × 38. (After Brady.)

The genus *Polymorphina* is remarkable for the fistulose branching processes which are developed in the later stages of the growth of the test. What relations these may have to the life-history has not been determined (Fig. 48, *c* and *d*).

Schlumberger has shown (50) that in *Siphogenerina glabra* the microspheric form tapers to a point at the initial end, and has 9-10 chambers arranged alternately before the uniserial mode of growth is assumed; while the megalospheric form is short, begins abruptly with a large central chamber, and has only three alternating chambers prior to the uniserial chambers.

## ORDER **Globigerinidea.**

In this group, as defined by Brady, the tests consist of a few inflated chambers arranged in a spiral manner. The members of it inhabit the surface waters of the ocean, furnishing an important constituent of the pelagic fauna; and their empty shells, falling to the bottom, form the main constituent of the "Globigerina ooze" (see p. 138).

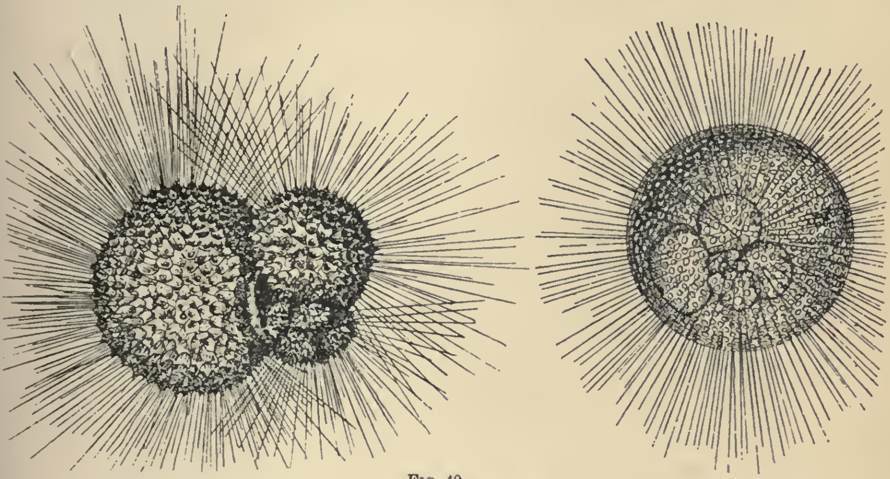

FIG. 49.

*Globigerina bulloides*, d'Orb. (to left), and *Orbulina universa*, d'Orb. (to right). (From Rhumbler, 38.) The figure of *G. bulloides* represents the test as seen from the superior surface. The specimen departs from the normal in possessing an aperture on this aspect of the terminal chamber.

*Globigerina bulloides*, d'Orb. (Fig. 49), the most abundant species of the genus, has globular chambers forming a "rotaline" test, each opening by a separate orifice into the deep umbilical space on the "inferior"[1] surface. The chambers increase rapidly in size, as the series is followed, and there are three or four in the terminal convolution.

The walls of the chambers are perforated by pores, and at first are thin and smooth. As the shell increases in thickness, it generally becomes areolated on the surface, the deposit being greatest between the pores, so that these open into cup-shaped depressions, separated by ridges. In many, but not all pelagic specimens the shell is produced on all sides into radiating cylindrical spines which spring from the points where the ridges meet, and may exceed the diameter of the shell in length.[1]

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[1] See the characters of Rotalidae, p. 145.

A large proportion of the individuals, which in their earlier stages conform to the type of *Globigerina bulloides*, complete their growth under this form; but for others a different future is in store. Having attained a size which may be equal to that of the full-grown test of the other specimens, or may fall considerably short of it, these secrete a large spherical chamber which usually encloses the whole of the previously formed test, and is frequently more than double its diameter (Fig. 49, right-hand cut). The enclosed test is usually only connected with the investing wall at the points where its spines meet the wall and unite with it. The investing chamber is perforated by large pores, with a diameter of from 13-21 $\mu$, as well as by minute pores (5-6 $\mu$). The specimens which form the spherical chamber have been given the generic name *Orbulina*. It will be convenient to use the terms Orbulina chamber, and Globigerina chambers for the investing and the invested chambers respectively.

Unlike the Foraminifera which creep over the sea-bottom, the pelagic Globigerinae may be found invested with a vacuolated covering which is in part gelatinous (38, p. 6), though traversed by radiating pseudopodia which project beyond it. This envelops the whole shell and the bases of the spines, and has a spherical contour. It is probable that the Orbulina chamber is secreted at the surface of this vacuolated mass. A similar covering may be found investing the Orbulina shell in the later phases of the life-history.

As in the free *Globigerina*, the outer surface of the Orbulina chamber is beset with spines, which vary greatly in length, and specimens have been found, though rarely, the surface of which is areolated by ridges as in *Globigerina*. These have been separated under a distinct name—*O. porosa*, Terquem.

Rhumbler finds that, in pelagic specimens, the Globigerina chambers are always present within the Orbulina shell, though, owing probably to the solvent action of the sea-water, they are often reduced to fragments, or absent in bottom specimens.

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[1] Sir John Murray thus describes the appearance of the living animal: "In *Globigerina bulloides* (*hirsuta*) and *aequilateralis* the yellow-orange colour of the sarcode is due to the presence of numerous oval-shaped *xanthidiae* or 'yellow cells,' similar to those found in the Radiolaria. When the sarcode with these 'yellow cells' flows out of the foramina, and mounts between the numerous spines outside the shell, the whole presents a very striking object under the microscope; the transparent sarcode can be seen running up and down the long silk-like spines, and the 'yellow cells' seated at the base of these spines quite obscure the body of the shell." —*Nat. Science*, July 1897, p. 20.

The *Globigerina* chambers contained in the Orbulina shell differ from the free *Globigerina bulloides* in no respect, except in the extreme thinness of their walls, and Rhumbler (38) is inclined to separate the thin-walled shells hitherto classed under that species as the young stages of *Orbulina universa*, d'Orb. Rhumbler also points out, however, that in *Globigerina bulloides*, var. *triloba*, Reuss, which is characterised by the large size of the three last chambers, but not by the thinness of the shell, all variations are found between a terminal chamber which is folded back on its predecessor, and one which completely envelops the other chambers, as in *Orbulina*. The existence of these transitional forms in a variety with a shell of the usual thickness raises the question whether the *Globigerina* chambers enclosed in the *Orbulina* shell were so thin when free, or owe their thinness to the action of the protoplasm after their enclosure.

However this may be, we have the fact that some specimens classed as *Globigerina bulloides* end their individual existence in the *Globigerina* form, while other specimens, little or not at all distinguished from them in the early part of their growth, become enveloped by an *Orbulina* shell. These have been classed under a separate genus as *Orbulina universa*. The close resemblance between these two sets of specimens in the early stages of growth, and also between the *Orbulina* shell and that of the free *Globigerina*, in the varying development of the spines and the surface sculpture, strongly suggests that there is some more intimate relationship between them than that of allied genera, but what its precise nature may be is still very obscure.

A large inflated terminal chamber is also found in *Cymbalopora bulloides*, and in the littoral *Pulvinulina lateralis*, Terquem, and these, like the Orbulina chamber, are also perforated by large pores. *Cymbalopora* was taken in numbers by the *Challenger*, as a pelagic form, in the neighbourhood of coral reefs, and, according to Murray, every shell was filled with minute monadiform bodies.[1] This observation would suggest that the inflated chamber may go with the megalospheric form, but though Rhumbler finds a single large nucleus in all the specimens of *Orbulina* he examined, the same was true of the free Globigerinae. The size of the central chamber of the included test of *Orbulina* varies, according to Schacko (39), from 16-23 $\mu$ in diameter, while in the free *Globigerina* it varies from 7-20 $\mu$. Neither in the size of the central chamber, nor in the character of the nuclei, therefore, have we at present direct evidence for dimorphism among these animals. As to the modes of reproduction of *Globi-*

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[1] Brady (3), p. 639, footnote.

*gerina* or *Orbulina* almost nothing of a definite character is known.[1]

### ORDER **Rotalidea.**

Schlumberger has found *Rotalina pleurostomata*, Schlumb. (= *Pulvinulina partschiana*, d'Orb.), to be dimorphic (51), and I have found the same in *Rotalia beccarii*, Linn. Among seven examples of this species six were megalospheric, and one microspheric. In these $M = 55\ \mu$ (limits of variation 37 and 65 $\mu$), and $m = 13\ \mu$. There appears to be no difference in the mode of arrangement of the chambers in the two forms, but the nuclear characters agree with those of *Polystomella*. I have observed the production of a brood of megalospheric young by a microspheric parent of this species, the process agreeing with that described in Polystomella (20, p. 436).

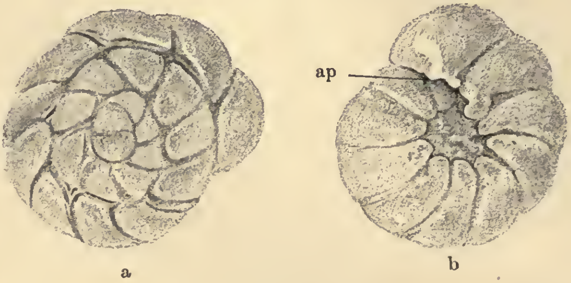

FIG. 50.
*Rotalia beccarii*, L., seen from the superior (a) and inferior (b) surfaces. *ap*, aperture. × 30.

Similarly in *Calcarina hispida*, Brady, $M = 49\ \mu$ (limits of variation in twelve examples 39 and 59 $\mu$), $m = 13\ \mu$ (limits 12 and 14 $\mu$), and here, again, I found a microspheric specimen with megalospheric young, which in this case were contained within the parent shell.

The rose-coloured adherent tests of *Polytrema* are common on coral and other objects from tropical and sub-tropical shores. They may be depressed and encrusting, but frequently rise from an expanded base into arborescent forms. They are built up for the most part of numerous successive laminae of hard perforated shell substance, produced inwards at short intervals into hollow pillars (Fig. 51, *a*, *p*), which are connected with the underlying shell lamina. The openings of the pillars of the superficial layer give rise to the deep pitting of the surface from which the genus is named. Except in the early stages of growth there is no subdivision of the test into definite chambers. The protoplasm is contained between the laminae, and in irregular spaces which occupy the axes of the branches; it communicates with the exterior by the numerous perforations in the laminae, and at the ends of the branches where the axial spaces open widely. Their mouths are often beset with sponge spicules, which appear to be used as a temporary scaffolding for the support of the extended pseudopodia, in advance of the proper wall.

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[1] The fact that the Orbulina chamber is formed in the later stages of growth of the individual, which in its earlier stages formed the enclosed Globigerina chambers, was first definitely stated by Rhumbler (34). The view had, however, been previously suggested by Major Owen (32, p. 147).

At the base, however, in contact with, or close to, the object to which the *Polytrema* adheres, a spiral group of chambers is found —the initial stage of the test (Fig. 51, *a*, *R*, and *b* and *c*). These initial chambers have the thick coarsely perforated walls, the abundant chitinous element, and the spiral arrangement characteristic of the order Rotalidea.

In ten specimens of the *megalospheric* form, I find that *M* varies from 110 to 29 $\mu$, its average value being 51 $\mu$. In these specimens there are generally three chambers, following the megalosphere, arranged in a simple spiral (Fig. 51, *c*); the fourth chamber usually communicates by apertures with two or more chambers, and after this the arrangement becomes more and more irregular, all distinction between the chambers and connecting passages is gradually lost, and the laminate structure of the test is attained.

I have not happened to meet with specimens of the *microspheric* form, but this has been described by Merkel (23)[1] who finds that the microsphere (size not given) is succeeded by a regular spiral of some eleven chambers, before the chambers assume the irregular transitional character.

In some cases the spiral of initial chambers is separated from the supporting object by a layer of small chambers of the irregular transitional form, and Schlumberger (56) has found in sand from the Azores small examples of the megalospheric form as free globular tests, consisting of the large initial chambers invested on all sides with a layer of small ones. It is evident, therefore, that *Polytrema* may pass through a more or less prolonged period of free life before it becomes adherent.

Merkel found the nuclear condition to agree with that of *Polystomella*, three examples of the megalospheric form containing a single large nucleus lying in the megalosphere or an adjoining chamber, while in one of the microspheric form four nuclei were counted.

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[1] In the megalospheric form, Merkel describes the megalosphere as communicating directly with some three of the surrounding chambers—a condition which I have not met with.

*Polytrema* was associated by the earlier naturalists with various animals classed as "zoophytes," and was included by Pallas and Gmelin in the genus *Millepora*. Its Rhizopod affinities were first recognised by Dujardin, and its relation to *Tinoporus* by Carpenter.

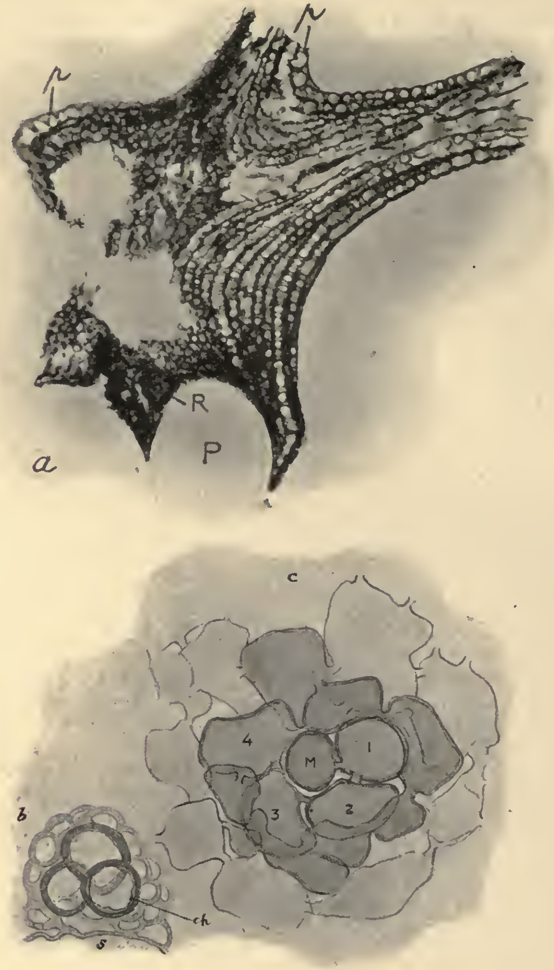

Fig. 51.

*Polytrema miniaceum*, Linn. *a*, section of the test passing along the axis of a branch, and through the stem of a Polyzoan (P), to which the test was adherent; *p*, the hollow pillars between the laminae; R, the group of rotaloid chambers, the initial stage of the test, × 20. *b*, the group of rotaloid chambers (*a*, R), × 78; *s*, the surface of attachment to the Polyzoan; *ch*, the chitinous lining of a chamber. *c*, central part of the base of a young test decalcified and treated with caustic potash, seen from the surface of attachment. The chitinous walls of the chambers remain. M, the megalosphere, 1-4, the first four of the spiral series of chambers, × 78.

Max Schultze was the first to demonstrate the spiral arrangement of the early chambers, and its dimorphic character was shown, as we have seen, by Merkel.

The life-histories of *Patellina corrugata*, Will, and *Discorbina globularis*, d'Orb., as exhibited by specimens living in aquaria, have been investigated by Schaudinn (45). Ordinarily the protoplasm contains many granules which, during life, obscure the nuclei, but by excluding animal food, and limiting the diet to the diatoms growing on the sides of the vessels, Schaudinn succeeded in rendering the nuclei visible, so that their changes could be followed in the living animal.

The form of reproduction observed was that comparable with the production of broods of megalospheric young by a megalospheric parent, and Schaudinn's account of the changes which the nuclei undergo is the fullest which we yet have of their behaviour in this phase of the life-history of the Foraminifera.

All the specimens which came under notice contained a single nucleus in their early stages. As the reproductive phase approached the nucleus became segregated into a number of parts (usually 7-10), which were dispersed in the protoplasm, and in some cases became subdivided by a similar process, so that there may be as many as 30 nuclei of unequal sizes. The protoplasm becomes divided up about the nuclei into masses proportional to them in size, and the young thus produced repeat in turn the same cycle of development. In *Discorbina* the division to form the young occurs within the parent test, from which they escape by the resorption of its walls. In *Patellina* it occurs in the large umbilical space, *i.e.* outside the parent test. Schaudinn is inclined to the conclusion that in these species the stage in which zoospores are produced has been lost from the life-history, and that reproduction takes place only in the manner described. Thus he regards these species as having been originally dimorphic, but now monomorphic.

I have measured the central chambers of a number of stained and mounted specimens of *Discorbina globularis* collected from the seashore, and the results are shown in Fig. 52. It will be noticed that in this species the central chamber is on the whole remarkably small. In the great majority it varies in size from 12 to 31 $\mu$, the average of 159 specimens being 19 $\mu$. In one case it was only 9 $\mu$ in diameter.

In this species the chitinous element of the shell is very abundant, and forms an obstacle to the penetration of staining reagents, but 54 of these specimens afford an indication of the nuclear condition. In 48, including two with a central chamber 16 $\mu$ in diameter, a single nucleus is present, and in one of the remainder a large nucleus is killed in the process of breaking up into fragments. In the specimen, the central chamber of which measures 9 $\mu$ in diameter, 6 nuclei are clearly seen. In the 4 remaining multinuclear specimens the mean diameters of the central chambers are 22, 18, 12, and 12 $\mu$.

Now it is possible that all these examples of *Discorbina* belong to a single series illustrating the phases of the life-history which Schaudinn has followed in aquaria, but the coincidence of the occurrence of the multinuclear condition with the very small central chamber, 9 $\mu$ in diameter, suggests that *Discorbina* is, like its allies, a dimorphic form. On this view we may regard the specimens with a single nucleus as megalospheric, and the specimen with (at least) 6 nuclei and a central chamber 9 $\mu$ in diameter as microspheric. The remaining multinuclear specimens may consist of megalospheric individuals, the nucleus of which is breaking up prior to reproduction, or of microspheric individuals with a larger microsphere, or, and more probably, of both kinds.

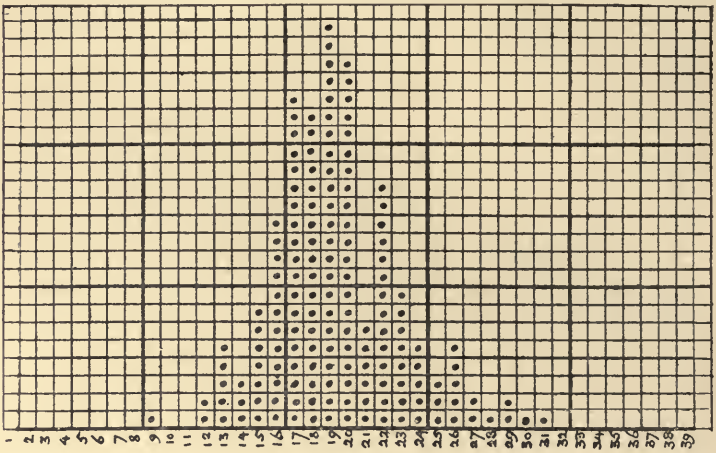

Fig. 52.

Table showing the dimensions in micromillimeters of the central chambers of 159 specimens of *Discorbina globularis*, d'Orb.

On this view the form of reproduction which Schaudinn described in *Discorbina* is the production of megalospheric young by a megalospheric parent which is, as we have seen, of frequent occurrence in other genera.

The formation of zoospores by the megalospheric parent was not observed among the specimens kept in aquaria, but we are still at liberty to suppose that this phase of the life-history may occur in the natural state.

*Truncatulina lobatula*, W. and J., affords another instance of the approximation of the megalosphere to the size of the microsphere. Thus in 13 examples I found 12 to be megalospheric and the value of $M$ to be, on an average, 28 $\mu$, varying from 36 to 15 $\mu$. The other specimen is microspheric, and $m = 11\ \mu$. The nuclear characters corresponded to those described in *Polystomella* (20).

*Plastogamy.*—This remarkable and little understood process which has been observed in other groups of Protozoa was found by Schaudinn to be frequently associated with the reproduction of *Patellina* and *Discorbina.* In the former the pseudopodia of two individuals that have come, apparently by chance, into juxtaposition fuse, and form a uniting band which increases in thickness until all the extruded protoplasm is involved in it, and the tests are drawn close together. The nucleus in each meanwhile divides in the manner above described. Gradually the protoplasm of both emerges into the space between the bases of the approximated tests and the surface to which they are attached, and then, as in the reproduction of a single individual, divides up about the nuclei to form a brood of young (Fig. 53). As many as five individuals may thus unite. In no case did Schaudinn observe any fusion between the original nuclei or the fragments into which they divided. He also found that the process only occurred when the nuclei of the individuals which met were in the same phase of

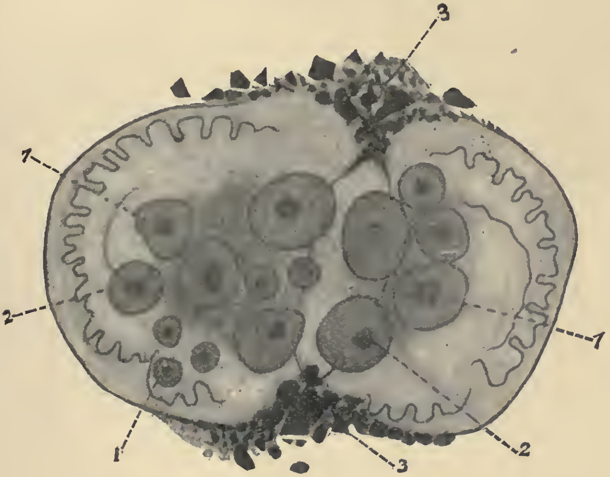

Fig. 53.

View from the under side of two specimens of *Patellina corrugata*, Will., which have united in plastogamy prior to the breaking-up of the united protoplasm to form a brood of young. 1, young of varying size; 2, nucleus of a young individual; 3, accumulations of detritus. (After Schaudinn, 45.)

development; thus a one-nucleated individual and an individual whose nucleus had begun to divide would not unite.

In *Discorbina* a similar process was observed; but in this case the two individuals came together base to base, and the pair wandered about for a considerable time before the young were produced. In some cases a deposit of lime between the opposed bases occurred in the interval, so that after the escape of the young the empty parent shells remained united together. The remarkable pairs of shells which have been observed in *Discorbina*, *Textularia*, and *Bulimina* (Fig. 54) are, probably, thus explained.

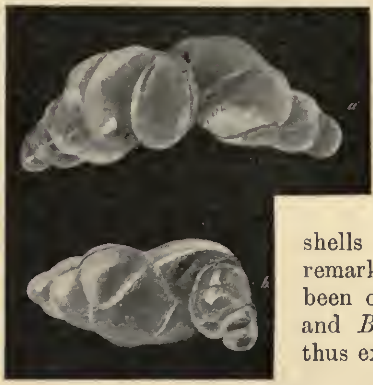

Fig. 54.

Paired tests of a species of *Bulimina* from Delos. In *a* the paired individuals are of equal, in *b* of very unequal size. From specimens kindly given me by Mr. H. Sidebottom.

## Order **Nummulitidea.**

The members of this order are distinguished by their bilaterally symmetrical tests, which in the early stages or throughout growth are arranged on the spiral plan; by the double character of the septa between the chambers, containing branches of the highly developed canal system interposed between the laminae; by their hard perforated walls; and by the slit-like aperture (subdivided in *Polystomella*) situated between the inner margin of the septum and the wall of the previous convolution.

The structure of *Polystomella* is described above (pp. 62 *et seq.*). *Nonionina* is a simpler form of the same type, characterised by the scantiness of the umbilical deposit, the absence of retral processes, and the fact that the aperture is not subdivided into pores, as in *Polystomella*, but remains a simple slit.

*Amphistegina* is transitional in structure between the Rotalidea and Nummulitidea; it has simple septa, and the test is not truly symmetrical, the spire being (as in the Rotalidea) slightly helicoid and the aperture on one (the "inferior") side of the median plane. In the marked development of the alar prolongations it approaches the genus *Nummulites.*

In *Operculina* (Fig. 55) the chambers are simple and disposed in an expanding spiral, some three or four convolutions completing the test. The earlier chambers are produced to a greater or less extent into alar prolongations, and thus a boss-like umbo is formed at the centre; but the later chambers are simply applied to the margin of the previous convolution, and have a large radial extent. The aperture is crescentic and undivided, but is supplemented by pores distributed along the septum.

The canal system is highly developed, a plexus of canals, in connection with the meridional vessels, running in a keel-like thickening at the outer rim of the test.

A sample of sand obtained by Mr. J. Stanley Gardiner from Suvadiva in the Maldive Archipelago consists for the most part of the tests of *Operculina complanata* and *Heterostegina depressa*, d'Orb. Of the former I have found two specimens of the *microspheric* form, in both of which $m = 27\ \mu$, and the second chamber is very minute (Fig. 55, B).

In five specimens of the megalospheric form the values of $M$ vary from 45 to 63 $\mu$ and have an average of 54 $\mu$.

I have not observed that the tests of the two forms of this species are distinguished by a difference in size.

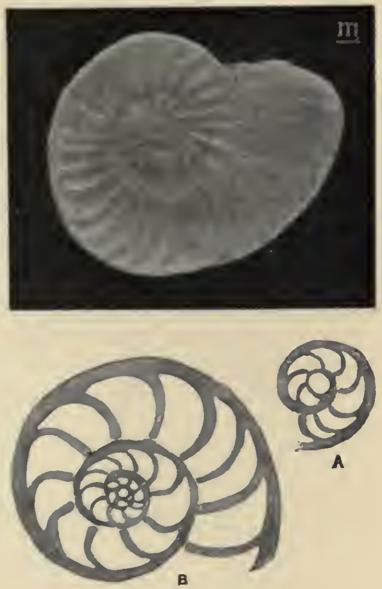

FIG. 55.

*Operculina complanata*, Def. m, a complete test, × 8; A, central part of section of megalospheric form; B, of the microspheric form. (A and B, × 50.)

In *Nummulites* the chambers are of very small extent in a radial direction (Fig. 6), so that each convolution adds little to the diameter of the test, and the outline of the latter is nearly circular. The number of the convolutions is however very large. The alar prolongations, on the other hand, are highly developed, and extend nearly to the centre. As the chambers of each successive convolution are thus produced, the result is that the tests are strongly biconvex, the spiral axis measuring from one-third to three-quarters of the diameter. The alar prolongations of the chambers may be directed straight towards the spiral axis (radiate type) or take a sinuous course (sinuate type), or they may be replaced by a number of separate chamberlets forming when exposed in worn specimens a network over the surface (reticulate type). The aperture and canal system resemble those of *Operculina*.

The microspheric form attains, as we have seen, a much greater size than the megalospheric (Fig. 5). I am not aware of any record of the actual size of the microsphere.

In the megalospheric forms $M$ is very large, attaining in some cases 1 mm.

While *Operculina* is closely connected on the one hand with *Nummulites*, it forms, on the other, the simplest term of a series —*Operculina*, *Heterostegina*, *Cycloclypeus*, which presents among the Nummulitidea a remarkably complete parallel to the *Peneroplis*, *Orbiculina*, *Orbitolites* series in the Miliolidea.

In *Heterostegina* (Fig. 56) the arrangement of the chambers is spiral, though they become somewhat more embracing as age advances. The chambers which are first formed are simple, as in *Operculina*, but they soon become subdivided by partitions which are disposed perpendicularly to the plane of the spiral, and, on the whole, transverse to the long diameter of the chambers. The chambers are thus subdivided into more or less quadrangular chamberlets. As in *Operculina*, the chambers of the inner convolutions are produced into alar prolongations (which are, however, not subdivided into chamberlets), while the later chambers are simply applied to the edge of the preceding convolution. The arrangement thus presents considerable resemblance to that of *Orbiculina*, but in addition to the presence of the canal system, perforate walls, and double septa, there is also a marked difference in the mode of communication of the chamberlets, for here the adjacent chamberlets of a chamber do not communicate directly with one another, but each communicates as a rule with two chamberlets of the preceding and with two of the succeeding chambers. (These communications are not displayed in the sections figured, but may be readily seen in the protoplasmic casts of decalcified specimens.)

The canal system is well developed and resembles that of *Operculina*, a marginal plexus being present here also.

In the sample of sand from the Maldive Islands, above mentioned, the great majority of the specimens of *Heterostegina* range from a small size up to about 4 mm. in their larger diameter (Fig. 56, A), but a few far exceed the rest, attaining a diameter of 10 or more mm. (Fig. 56, B). I am unable to recognise any difference in the external appearance of the two forms, beyond that in size, and the peculiar shape of the large specimens caused by the greater width of the terminal convolution. On making sections of the tests it is found that the large specimens are microspheric and the smaller ones megalospheric.

In two specimens of the former $m = 27\ \mu$ in both, and a spiral of some 36 simple chambers succeeds before the septa appear, dividing the chambers into chamberlets (Fig. 56, B′).

In the megalospheric form $M$ varies in four cases from 70 to

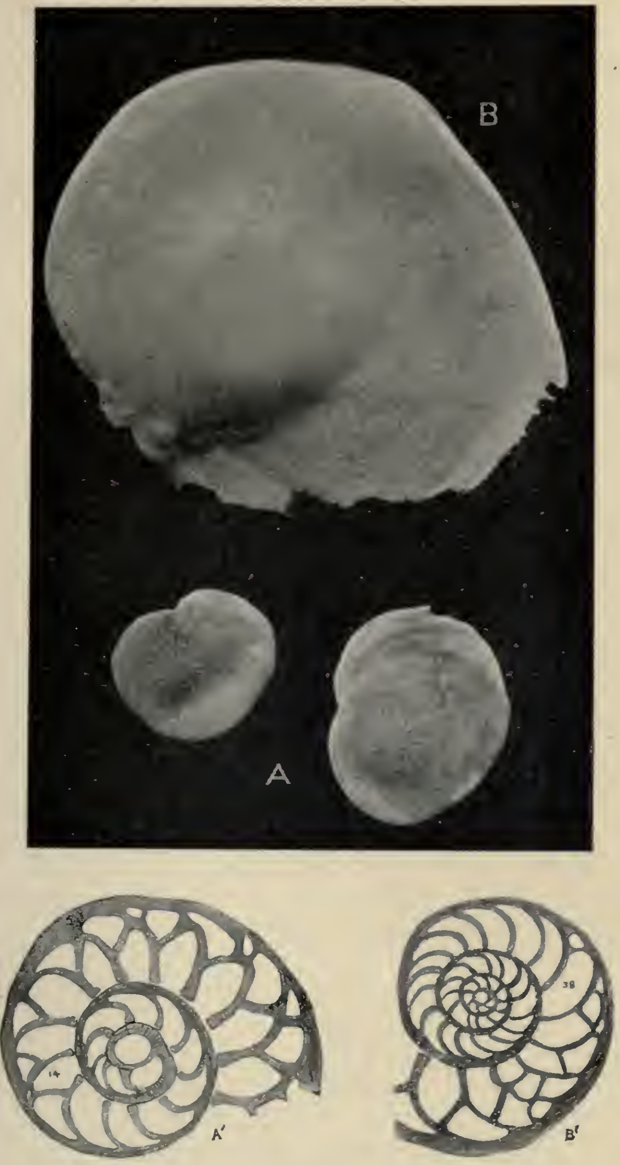

Fig. 56.

*Heterostegina depressa,* d'Orb. A and B the megalospheric and microspheric forms, × 8. A′, B′, central regions of sections of these tests in the median plane, × 50. The figures 14 and 38 mark the first of the subdivided chambers, in the two forms respectively. The canal system is barely indicated in this figure and in figure 55.

80 $\mu$, and the number of single chambers is 9 to 12. In some cases the chamber which succeeds the megalosphere is considerably larger than those which immediately follow (Fig. 56, A′).

We thus have in this sand from the Maldives a difference in size between the two forms of *Heterostegina* similar to that found in the Nummulitic formations of the Eocene period.[1]

In the third genus of the series, represented by the species *Cycloclypeus carpenteri*, the great majority of the individuals do not exceed 12 mm. in diameter, but some attain the large size of 64 mm.

It is very probable, from analogy with other genera, that the specimens which attain the large size are microspheric; those of smaller size are, in the specimens which I have examined, megalospheric.

The only specimen (Figs. 57, B, and 58) of the *microspheric* form which I have examined is a section.[2] In it the microsphere measures 29 $\mu$, and is followed by 9 single chambers arranged in a spiral. The chambers then become subdivided, as in *Heterostegina*. After being disposed at first in a spiral, they gradually extend round a larger and larger part of the circumference of the test until they completely encircle it, and the arrangement becomes annular. The twenty-fifth chamber from the microsphere is, in this specimen, the first to complete the circle.

In the *megalospheric* form the centre is occupied by a structure somewhat resembling the "primitive disc" of *Orbitolites complanata* (p. 106). It is, however, differently constituted. The megalosphere is very large, its average mean diameter in 9 cases being 245 $\mu$, and the extremes 465 and 175 $\mu$. It communicates by a narrow neck with a large chamber which is applied to the megalosphere for about half its circumference, and communicates in turn with another large chamber.

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[1] Chapman (10, p. 19) believes that he has found the dimorphic forms of *Heterostegina*, and identifies them with the biconvex and the compressed varieties described by Brady. He finds that the size of the full-grown megalospheric test is greater than that of the microspheric, a result which he recognises as unusual. The relative sizes of $M$ and $m$ are said to be in the proportion of 3:2, and I learn from Mr. Chapman, by letter, that the actual diameters were 125 and 65 $\mu$ respectively. These results are so far at variance with the phenomena of dimorphism in general, and with my own in this species, that it appears probable that the individuals with the smaller central chamber were megalospheric specimens with rather smaller megalospheres, and that Mr. Chapman did not meet with the microspheric form.

[2] I have to thank Professor J. W. Judd for the opportunity of examining and figuring this section. The specimen was obtained at Funafuti, in the Pacific, and the section was prepared by Mr. Chapman, and figured by him (10, Pl. III. Fig. 2) on a small scale. In this paper the specimen is regarded as an unusual example of the megalospheric form, but I understand, by letter, from Mr. Chapman that he is now inclined to reconsider this view. Fig. 58 is prepared from a photograph of the central region, on a larger scale, and Fig. 57, B, shows the arrangement of the chambers more clearly.

The arrangement of the chambers which succeed varies in different specimens. In some (as in Fig. 57, A) a succession of about six subdivided "heterostegine" chambers follows, which become more and more embracing, until they extend completely round the previously formed chambers. The annular arrangement once attained is continued, though not without irregularities of growth, till the test is complete. The mode of communication of

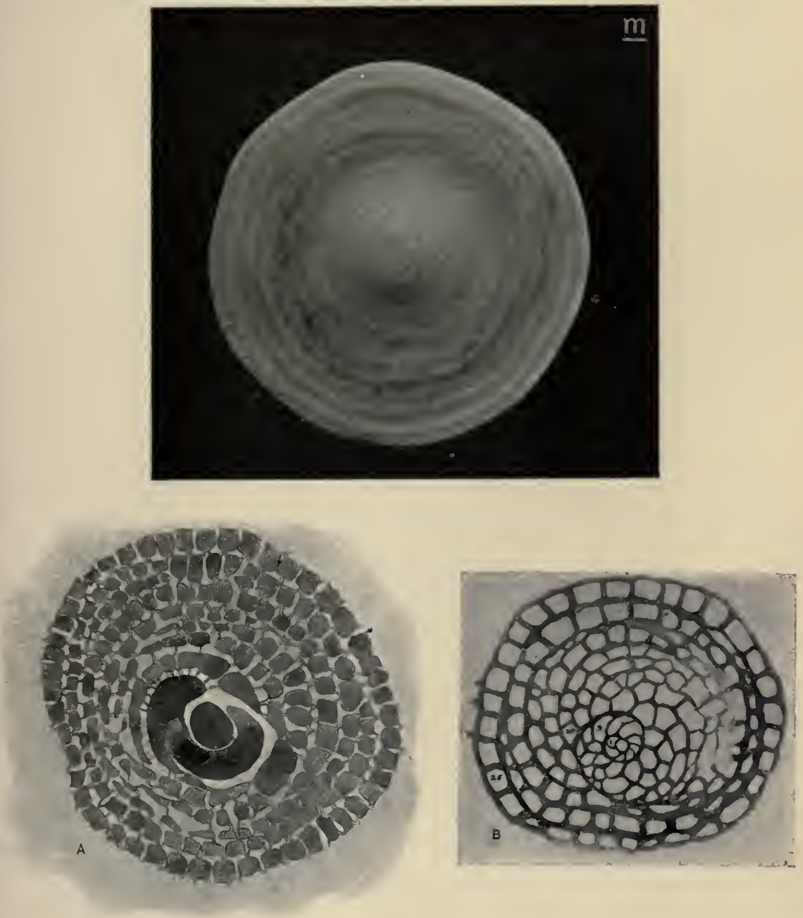

Fig. 57.

*Cycloclypeus carpenteri*, Brady. m, a complete test, × 8. A, central region of a decalcified specimen of the megalospheric form, × 35. B, central region of a section of the test of the microspheric form, × 50. The canal system is not seen in these figures. The figures 1 and 9 in B mark the first and last of the undivided chambers, 20 is a heterostegine chamber, and 25 the first of the annular chambers.

the chamberlets with one another is similar to that described in *Heterostegina*. The variations on this arrangement which occur result from a more speedy attainment, in different degrees, of the cyclical growth. Where the nuclear characters have been recognised, a single large nucleus was found in one of the large central chambers of the megalospheric form.

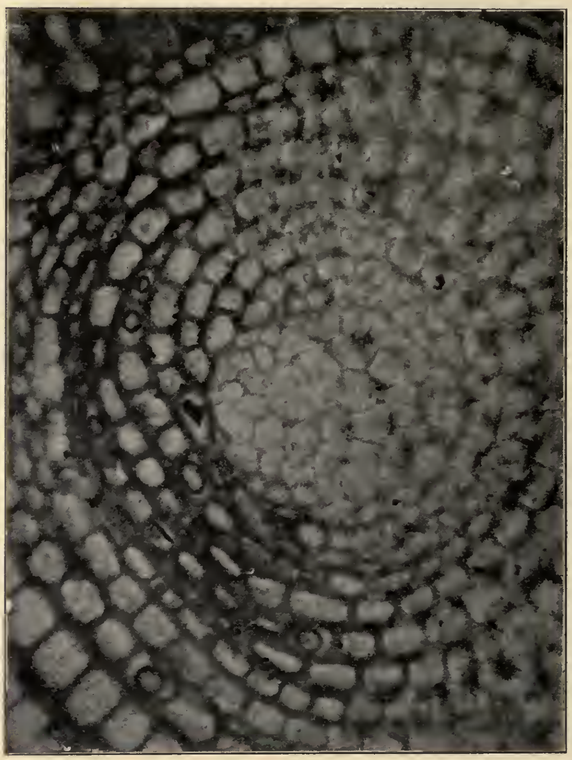

FIG. 58.

Photograph of the central part of the section of *Cycloclypeus carpenteri* (microspheric) represented in Fig. 57, B.

Looking back on the evidence furnished by these three genera we find that *Operculina* is built on the same plan in both microspheric and megalospheric forms; that *Heterostegina* repeats the operculine condition in both forms, though the number of undivided chambers is greater in the microspheric form than in the megalospheric; and that *Cycloclypeus* repeats both the operculine and heterostegine conditions in the microspheric form, while in the megalospheric the operculine stage is omitted or represented only by the two large chambers which succeed the megalosphere, and the heterostegine stage is considerably shortened. In fact, we find the same tendency in the megalospheric form to abridge or omit the stages repeated by the microspheric form as we have seen in other cases.

The genus *Fusulina* is represented by a series of forms which abound in the Carboniferous and Permian rocks in Russia, North America, Sumatra, and elsewhere. By their perforate walls, their bilateral symmetry about a median plane, and the character of the aperture, which is a slit left between the margin of the septum and the surface of the preceding convolution, they appear to belong to the Nummuline stock. Like the species of *Alveolina* they present varying degrees of elongation in the direction of the spiral axis from the biconvex discs of *F. aequalis* (Fig. 59, A) to the fusiform tests of *F. cyclindrica* (D).

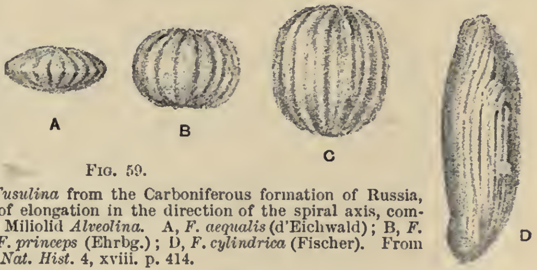

Fig. 59.

Forms of the genus *Fusulina* from the Carboniferous formation of Russia, showing varying degrees of elongation in the direction of the spiral axis, comparable with those of the Miliolid *Alveolina*. A, *F. aequalis* (d'Eichwald); B, *F. sphaeroidea* (Ehrbg.); C, *F. princeps* (Ehrbg.); D, *F. cylindrica* (Fischer). From Brady, *Ann. and Mag. of Nat. Hist.* 4, xviii. p. 414.

The megalospheric and microspheric forms of *Fusulina* have been recognised by Schlumberger (58).

We may now take a brief survey of some of the main phenomena which have presented themselves in the several groups.

Among the species of Foraminifera we meet with modifications of form of three kinds. There is the modification which occurs during the growth of an individual, producing the "*multiform*" condition of test. There is the difference among individuals dependent on their mode of origin, whether from a megalosphere or a microsphere, which finds its expression in *dimorphism*. Finally, there is the variation commonly presented to a greater or less extent by animals and plants, the departure of the individual in different degrees from the type form of the species.

We may consider these three kinds of modification in the reverse order.

*The Variation of the Foraminifera.*—It has long been recognised by systematists that in many cases the limits of the characters of the species of Foraminifera do not admit of being drawn with any exactness. This view was insisted on by Carpenter, who, in the "*Challenger*" *Report* on *Orbitolites* (p. 9), quotes with approval the doctrine that among the porcellanous and vitreous Foraminifera "everything passes into everything else."

Carpenter, indeed, held (*l.c.* p. 8) that "the ordinary notion of *species* as assemblages of individuals marked out from each other by definite characters that have been genetically transmitted from original prototypes similarly distinguished, is quite inapplicable to the group of the Foraminifera." And again, in the *Introduction* we read (8, p. 56):—"The impracticability of applying the ordinary method of definition to the *genera* of the Foraminifera becomes an absolute impossibility in regard to *species*. For whether or not there really exist in this group generic assemblages capable of being strictly limited by well-marked boundaries, it may be affirmed with certainty that among the forms of which such assemblages are composed, it is the exception, not the rule, to find one which is so isolated from the rest by any constant and definite peculiarity, as to have the least claim to rank as a *natural* species."

The question, however, appears to be not whether all intermediate terms do or do not exist between dissimilar forms, but whether the whole body of forms, as they occur in nature, tend to group themselves, or are aggregated about certain centres. If this is the fact, and the forms, as they occur in nature, are disposed not in a continuous series, but in a discontinuous one, the large number of individuals being grouped about distinct centres, we have the phenomenon which is comparable with that of species in other animals and in plants, whether the centres are or are not connected by intermediate terms. To refuse to recognise the existence of these centres, because transitional forms exist between them, is to ignore an essential fact.

In a very large number of cases, at any rate, such centres do exist among the Foraminifera, as among other organised beings, and the characters of the middle individuals of them are those of the species.

The *dimorphism of Foraminifera* depends, as we have seen, on two modes of reproduction, which recur in a cycle of generations. The megalospheric form arises by the multiple fission of a single parent, while there are strong grounds for concluding that the microspheric form arises from a zygote, formed by the conjugation of zoospores.

The phenomena of dimorphism are exhibited in the size of the initial chambers, in the nuclear characters, in the mode of reproduction, and, often, in the plan of growth. In most of the species of Foraminifera in which we have evidence of the sizes of the initial chambers, they are strongly contrasted in the two forms, although in some, as in *Peneroplis*, the size of the megalosphere may, in exceptional cases, fall below that of the microsphere. In this genus, as we have seen, the microspheric form is also to be distinguished by the absence of the spiral passage. In *Discorbina* and *Truncatulina* there is no such structural feature to distinguish the two forms, nor are they always to be recognised by the size of the central chambers. There is reason to believe, however, that they differ in nuclear characters, and mode of reproduction. Whether or not the two modes of reproduction prevail throughout the simpler forms of Foraminifera cannot at present be stated.

*The Multiform Condition.*—The significance of this condition is one of the most interesting problems presented by the Foraminifera. Perhaps the simplest case of its occurrence is that of *Polytrema* (p. 120). We have seen that in the earliest stages of life this organism is free, and secretes a test which resembles in many of its features that typical of the Rotalidae. After it has become adherent the rotaline mode of growth is exchanged for one adapted to the attached habit, and the test assumes an encrusting or arborescent form.

In the case of *Polytrema*, then, it seems clear that the arrangement of the chambers formed early in life repeats that of the rotaline stock from which it sprang, while the later chambers are disposed on a plan acquired as it has diverged from that stock.

Again, the more complex members (*Orbitolites* and *Cycloclypeus*) of the *Peneroplis-Orbitolites* and *Operculina-Cycloclypeus* series present excellent examples of the multiform condition. The facts that each of these is a series of closely related genera, and that the simpler members of each present in a permanent form the arrangement which is transitory in the growth of the more complex, appear to give substantial support to the view urged by Carpenter that the stages which we have called peneropline and orbiculine, operculine and heterostegine, in the growth of *Orbitolites* and *Cycloclypeus* respectively, are, in fact, repetitions in ontogeny of a phylogenetic history.

The application of this explanation to the multiform Miliolinidae appears less satisfactory because the earlier (quinqueloculine) plan of growth is somewhat more complex than the later, and we should not therefore expect it to be the more primitive. We need not assume, however, that the course of development has always been in the direction from simple to complex.

Closely connected with this question is the fact that the multiform condition is, as we have seen, much more pronounced in the microspheric than in the megalospheric form of a species. In a former paper I suggested (21) that a partial explanation of the contrast may be found in the difference in the mode of origin of the two forms.

The life-history of the Cladoceran *Leptodora hyalina*, appears to offer a similar contrast. Throughout the summer months broods of young are produced, which develop parthenogenetically and are hatched in the form of the parent. The resting winter egg, on the other hand, which develops as the result of fertilisation, emerges as a Nauplius larva—the form in which the members of such diverse families take their origin, and which, there is good reason to believe, repeats in several of its features the characters of the primitive *Crustacea.*

In the case of *Leptodora* we see that after, and apparently as the result of, fertilisation the organism "casts back" in its development, repeating primitive features which are abbreviated or absent in the development of the form arising without a sexual process. Now although the megalosphere of the Foraminifera, the product of the multiple fission of the parent, may not be strictly comparable with the unfertilised egg of *Leptodora*, it has, at least, this in common with it, that it arises asexually, while it is probable that the microspheric form arises from the conjugation of gametes, a process comparable to the fertilisation of the Metazoa. In the paper referred to it was suggested that the accentuation of the multiform character of the microspheric form of the Foraminifera, as compared with the megalospheric, is likewise dependent on the process of fertilisation.

It still appears to me possible that the explanation may be found in the direction indicated, but that this is not the complete solution is shown by consideration of the Initial Polymorphism displayed by the megalospheric forms of several species. In *Idalina* and *Orbiculina* we have seen that the extent to which the phases of growth which occur in the development of the microspheric form are repeated by the megalospheric form varies in different individuals, and that it is correlated with the size of the megalosphere—individuals with small megalospheres repeating these phases more completely than those with large megalospheres. What the cause of this correlation may be appears entirely obscure, but it is evident that if among the megalospheric forms, arising asexually, the completeness of the repetition of the earlier phases depends on the size of the central chamber, we are not at liberty to refer the completeness of their repetition in the microspheric form wholly to its sexual origin.

In his sketch of a natural classification of the Foraminifera (36 and 37) Rhumbler takes altogether different views of the phenomena we have been considering, and the classification proposed as the result has been adopted by Lang in the new edition of his *Lehrbuch.*

In Rhumbler's view "Festigkeitsauslese," the selection of the forms of test best adapted to resist mechanical stress, is regarded as the chief factor which has dominated the differentiation of the Foraminifera, and several series of genera, such as the *Nodosaria-Cristellaria* and the *Biloculina-Quinqueloculina* series, are given as examples of a "Festigkeitskala" in which varying degrees of resisting power have been attained.

In the biformed and triformed tests the early chambers are regarded as arranged on a higher (*i.e.* more resisting) plan than those added later, and hence it is concluded that in the ontogeny of the Foraminifera the order of the appearance of the more primitive and the later acquired characters is the reverse of that so general in the development of other animals, the earlier arrangement representing the form towards which the race is advancing, the later retaining the characters which will ultimately be discarded.

This reversal of the usual order is attributed to the great delicacy of the young test, to compensate for which a more compact arrangement of the chambers has been acquired. In the later stages of growth, owing to the larger bulk of the protoplasm, the chamber walls can be secreted of such a thickness as to counterbalance the mechanical weakness of their arrangement.

The contrast in the modes of growth of the megalospheric and microspheric forms is similarly explained, the small size of the latter in the early stages of growth calling for an arrangement, which is less urgently needed in the later stages, or by the megalospheric form. In the more perfected genera, however (as *Quinqueloculina*), the tests of the forms of both generations are moulded on the most compact type.

Thus Rhumbler, like Carpenter, regards the multiform tests of Foraminifera as of great value in tracing out phylogeny, but for precisely opposite reasons, for while Carpenter considers the early phases as representing a stage through which the stock has passed, Rhumbler sees in them the higher stage towards which it is advancing.

As will be gathered from what has gone before, it does not appear to me that sufficient reason has been shown for discarding the view of Carpenter.

Another remarkable phenomenon met with among the Foraminifera is that of *Isomorphism.* It may be defined as the occurrence under similar external forms of species belonging to distinct stocks.

Perhaps the most striking instance of it is presented by the Miliolidea and Nummulitidea. It has been pointed out how in the latter family the series *Operculina*, *Heterostegina*, *Cycloclypeus* runs parallel with the *Peneroplis*, *Orbiculina*, *Orbitolites* series of the Miliolidea, and we have seen that in *Heterostegina*, as well as in *Polystomella* and other allied genera, the tests are to some degree extended in the spiral axis owing to the equitant character of the chambers. The resemblance between the corresponding terms in the two series is rendered all the more remarkable by consideration of the forms included in the genus *Fusulina*, which, at the period when the Carboniferous and Permian rocks were deposited, had undergone elongation in the direction of the spiral axis and been differentiated into a series of forms—biconvex, obovate, spheroidal, and fusiform—closely comparable with those assumed by the species of *Alveolina* of the Tertiary period and the present day (cp. Figs. 42 and 59).[1]

*Distribution.*—From this point of view the Foraminifera may be divided into two classes—the attached or bottom-living and pelagic forms. While by far the greater number of genera and species belong to the former, the numbers of individuals of the latter are enormously great.

The Pelagic Foraminifera belong to the genera *Globigerina* (with its connected form *Orbulina*), *Hastigerina*, *Pullenia*, *Sphaeroidina*, and *Candeina*—forming the order Globigerinidea—and *Pulvinulina* and *Cymbalopora* among the Rotalidea. The pelagic habit of these forms, though it had previously been recognised by M'Donald and Major Owen, was first clearly established by the naturalists of the *Challenger*.

The species which are found at the surface extend down to considerable depths, but whether they may actually live on the bottom of the ocean is still, in spite of much discussion, undecided. They congregate at the surface at night, and partially withdraw from it during the day.

It is in the equatorial and temperate regions of the ocean that they most abound, the pelagic forms being represented in the arctic and antarctic seas by small species of *Globigerina: G. pachyderma* in the former, *G. dutertrei* in the latter.

Beneath this equatorial belt of warm water and its northern offset, the Gulf Stream, the empty tests of the pelagic Foraminifera constitute the main portion of the "Globigerina ooze," which forms the ocean floor down to a depth of 3000 fathoms. As this limit is approached the thinner tests disappear, and beyond it all calcareous constituents are removed by solution.[2]

The species of bottom-living Foraminifera have, on the whole, a very wide distribution. Some are cosmopolitan, ranging from arctic to tropical waters and from shore pools to the bottom of the great oceans. A large proportion of the genera, however, are restricted by depth and temperature. The shallow littoral waters of the tropics contain an abundant fauna, most of the members of which do not extend to colder seas. On the other hand, genera

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[1] The Lituolidea are described as "*isomorphous*" with various calcareous genera, but it is far from certain that the similarity in form does not depend on true affinity, in which case the term is not strictly applicable. *Loftusia*, among the Lituolidea, has a fusiform test, externally resembling the more elongated forms of the Fusulina and Alveolina series.

[2] Cp. Sir John Murray, "On the Distribution of the Pelagic Foraminifera," etc. *Natural Science*, July 1897, pp. 17-27.

(such as those of the Astrorhizidea) which abound in the arctic seas extend, as members of the abyssal fauna, along the ocean floor, to mingle in lower latitudes with the empty tests of the pelagic inhabitants of the warmer surface waters.

Notwithstanding the wide range of many species, there is some indication of a limitation of forms to definite areas—the formation of local faunas—comparable to that met with in the distribution of other animals and of plants. Thus in the warm shallow seas of the Malay Archipelago Mr. Millett finds the forms deviate in many instances from the ordinary structure of the Foraminifera.[1] In his reports hitherto published, dealing with the orders as far as and including the Lagenidea, he has described twenty-six new species and one new genus from this region.

*Geological Distribution.*—Representatives of four orders of the Foraminifera—Textularidea, Lagenidea, Rotalidea, and Globigerinidea—have been recognised in the Cambrian, the oldest of the "palaeozoic" formations. In the Carboniferous all the orders are represented except the Miliolidea—which have, however, been recognised in beds transitional between the Carboniferous and the Permian—the small and fragile Chilostomellidea, and the Gromiidea, whose slight tests we should hardly expect to find preserved. In the Carboniferous formation species of *Saccammina* and *Fusulina* give rise to extensive deposits. An abundant foraminiferal fauna has been found in many of the secondary formations, and the chalk of the later Cretaceous period is in large part built up of their tests, *Globigerina* being an abundant form as in the oozes of the existing ocean basins.

Foraminifera also enter largely into the composition of the earlier rocks of the Tertiary period. The Miliolidea here come into great prominence, and are represented by *Miliolina* (including *Quinqueloculina* and *Triloculina*), and its allies *Peneroplis*, *Orbitolites*, and *Alveolina*. Nummulites, which had already made their appearance in the Carboniferous period, also abounded in the warm shallow Eocene seas, and the Nummulitic limestones extend across the old world from the Pyrenees to China, attaining in some places thousands of feet in thickness.

It need hardly be pointed out that our knowledge of the life-history of the Foraminifera is still very far from complete. In the establishment of the prevalence throughout the higher groups of the phenomenon of dimorphism, dependent on different modes of reproduction, a substantial groundwork has been attained, but there remain many important questions of wide biological bearing on which we are very imperfectly informed.

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[1] Report on the Recent Foraminifera of the Malay Archipelago collected by Mr. A. Durrand, F.R.M.S., *Journ. Roy. Microscopical Soc.* 1898, p. 258.

There seems good reason to hope that the study of the plan of growth of both forms of the species during the early stages of their life-histories may throw light on the complicated problems of phylogeny. Until these early stages have received fuller attention, and we have arrived at a conclusion as to the relation of the early to the later stages of the multiform tests, efforts at forming a "natural classification" appear to be premature.

The classification adopted by Brady in his *Challenger* Monograph is given here, with slight modifications. I have followed Neumayr (30) in placing the Astrorhizidea before the Miliolidea as they appear to be more primitive forms. The Cycloclypeinae are merged with the Nummulitidae for the reasons given above.

It appears highly probable that the Lituolidea should be distributed (as Bütschli has done) among the calcareous forms which they resemble, but they are here left as arranged by Brady.

In conclusion I desire to express my thanks to my brother Mr. W. T. Lister, for his assistance in preparing the photographs of the shells of Foraminifera with which this article is illustrated. They were done with one of Zeiss' admirable instruments.

### ORDER 1. **Gromiidea.**

Test membranous, chitinous, or siliceous; smooth or encrusted with foreign bodies; with one or more pseudopodial apertures.

FAMILY 1. POLYSTOMATIDAE. Test with one or many openings. Genus *Myxotheca*, Schaudinn (Fig. 2). Test encrusted, openings many; marine. Here may be provisionally placed *Hyalopus*, Schaudinn (= *Gromia dujardinii*, M. Sch.). Test smooth, rounded, with one opening (Fig. 15), or branched, and with many; pseudopodia hyaline, with few or no anastomoses; multinucleate; marine.

FAMILY 2. MONOSTOMATIDAE. Test rounded or flask-shaped, with a single opening.

(*a*) Test smooth. Genera—*Gromia*, Duj. Test chitinous, usually flexible, mouth terminal; freshwater and marine (Fig. 1). *Lieberkühnia*, Clap. and L. Test very delicate, ovoid; mouth sub-terminal. *Mikrogromia*, R. Hertw. (*Cystophrys*, Archer) (Fig. 14). Test small, rigid, flask-shaped, bilaterally symmetrical, not filled by the protoplasm; pseudopodia springing from a short stalk of protoplasm; individuals often united by their pseudopodia into colonies. *Platoum*, F. E. Sch. Similar to *Mikrogromia*, but test more pointed. *Lecythium*, H. and L. Similar, but protoplasm filling the test. These four are freshwater genera.

(*b*) Test encrusted with foreign bodies. Genera—*Pseudodifflugia*, Schlumb. Resembles *Gromia*, but test encrusted; fresh and brackish water. *Diaphoropodon*, Archer. Test ovoid, built of loosely-united foreign bodies. Pseudopodia of two kinds: long, extended from the mouth; and short, hair-like (? true pseudopodia) between the particles of the test.

(*c*) Test built of chitinous or siliceous plates. Genera—*Euglypha*, Duj. (Fig. 3). Test elliptical or pear-shaped, with terminal mouth; built of circular or hexagonal siliceous plates; pseudopodia without anastomoses; freshwater. *Trinema*, Duj. Similar, but mouth on flattened lateral surface; freshwater. *Cyphoderia*, Schlumb. Test flask-shaped, built of small chitinous plates; fresh and brackish water. *Campascus*, Leidy Resembles *Cyphoderia*, but test encrusted; freshwater.

FAMILY 3. AMPHISTOMATIDAE. Test with an opening at either end.

(*a*) Test smooth. Genera—*Diplophrys*, Barker. Test roundish, very delicate; freshwater, and in manure. *Ditrema*, Archer. Similar, but test thicker; freshwater. *Shepheardella*, Siddall (Fig 16, 5). Test chitinous, long, and tubular, contracted to an opening at either end; marine.

(*b*) Test encrusted. Genus—*Amphitrema*, Archer (Fig. 16, 11). Barrel-shaped, test produced to a short neck round either opening; moor pools, Ireland.

## ORDER 2. **Astrorhizidea.**

Test invariably composite, usually of large size and monothalamous; often branched or radiate, sometimes segmented by constriction of the walls, but seldom or never truly septate; polythalamous forms never symmetrical.

FAMILY 1. ASTRORHIZIDAE. Walls thick, composed of loose sand or mud, very slightly cemented. Genera—*Astrorhiza*, Sandahl (Fig. 17, *a*). Test fusiform, or depressed and more or less stellate, and attaining a diameter of nearly one inch. *Pelosina*, Brady. *Storthosphaera*, F. E. Sch. *Dendrophrya*, Str. Wright. *Syringammina*, Brady. Test consisting of masses of branchings and anastomosing tubes.

FAMILY 2. PILULINIDAE. Monothalamous, wall thick, composed chiefly of felted sponge spicules. Genera—*Pilulina*, Carpenter (Fig. 17, *c*). Nearly spherical. *Technitella*, Norm. Oval. *Bathysiphon*, Sars. Tubular.

FAMILY 3. SACCAMMINIDAE. Chambers nearly spherical, walls thin, firmly cemented. Genera—*Saccammina*, M. Sars (Fig. 17, *b*). Globular, with distinct projecting aperture. *Psammosphaera fusca*, F. E. S., without a projecting aperture. Is regarded by Rhumbler as the young form of *Saccamminina sphaerica*. *Sorosphaera*, Brady. Many spherical adherent chambers, each with its own aperture.

FAMILY 4. RHABDAMMINIDAE. Test firmly cemented, of sand, often with sponge spicules intermixed, tubular, straight, radiate or branched, rarely segmented. Genera — *Jaculella*, Brady. Elongate, tapering. *Hyperammina*, Brady (Figs. 17, *d*, and 18). Elongated, tubular, simple or branched, sometimes commencing in a globular chamber. *Marsipella*, Norman. Fusiform or cylindrical. *Rhabdammina*, M. Sars. Rectilinear, radiate or branching, with or without a central chamber. *Aschemonella*, Brady. Test of inflated sacs, single or combined in series. *Rhizammina*, Brady. Fine chitino-arenaceous tubes, simple or branched. *Sagenella*, Brady. Adherent, branching tubes. *Botellina*, Carpenter. Test cylindrical of loose sand, with irregular cavities. *Haliphysema*, Bk. Test columnar, attached by a stalk, simple or branched, beset with sponge spicules (Fig. 19).

## ORDER 3. **Lituolidea.**

Test arenaceous, usually regular in contour, chambers of the polythalamous forms frequently labyrinthic. Comprises sandy isomorphs of the simple porcellanous and hyaline types (*Cornuspira*, *Peneroplis*, *Lagena*, *Nodosaria*, *Cristellaria*, *Globigerina*, *Rotalia*, *Nonionina*, etc.), together with some adherent species.

FAMILY 1. LITUOLIDAE. Test of coarse sand grains, rough externally; often labyrinthic. (*a*) Chambers non-labyrinthic. Genera—*Reophax*, Montf. Test free, composed of one flask-shaped chamber, or of several united into a straight, curved, or irregular line, never spiral. *Coskinolina*, Stache; *Haplophragmium*, Reuss. Test free, nautiloid, or crosier-shaped. *Placopsilina*, d'Orb. Chambers plano-convex, adherent. (*b*) Chambers labyrinthic. Genera—*Haplostiche*, Reuss. Test free, uniserial, never spiral. *Lituola*, Lamk. Test free, nautiloid, or crosier-shaped. *Bdelloidina*, Carter. Adherent.

FAMILY 2. TROCHAMMINIDAE. Test thin, composed of minute sand grains incorporated with calcareous or other cement; smooth, often polished externally. Genera—*Thurammina*, Brady. Test a single subspherical chamber. *Hippocrepina*, Parker; *Hormosina*, Brady. A rounded chamber, or several in a straight or curved series. *Ammodiscus*, Reuss. Test non-septate, coiled in a plano-spiral (resembling *Spirillina*) or otherwise. *Trochammina*, P. and J. Free or adherent, rotaliform, nautiloid or trochoid. *Carterina*, Brady. Test rotaliform, constructed of fusiform spicules, said to be proper to itself. *Webbina*, d'Orb. One or more adherent, stoloniferous chambers.

FAMILY 3. ENDOTHYRIDAE. Fossils. Test more calcareous and less sandy than in other Lituolidae, sometimes perforate. Genera—*Nodosinella*, Brady. Nodosariform. *Polyphragma*, Reuss. *Involutina*, Terq. *Endothyra*, Phil. *Bradyina*, Möll. *Stacheia*, Brady.

FAMILY 4. LOFTUSIIDAE. Test relatively large, lenticular, spherical or fusiform; arranged spirally, or in concentric layers; walls finely arenaceous and cancellated. Genera—*Cyclammina*, Brady. Nautiloid. *Loftusia*, Brady. Large, resembling *Alveolina* in contour. *Parkeria*, Carp. Large, spheroidal.

## ORDER 4. **Miliolidea.**

Test usually imperforate, normally calcareous and porcellanous, sometimes encrusted with sand; under starved conditions (*e.g.* in brackish water) becoming chitinous or chitino-arenaceous; at abyssal depths occasionally consisting of a thin, homogeneous, imperforate, siliceous film.

FAMILY 1. MILIOLINIDAE. Test of one or many chambers spirally arranged; in the many-chambered forms there are usually not more than two chambers in each convolution. (*a*) Test unsegmented, plano-spiral. Genus—*Cornuspira*, M. Sch. (Fig. 20). (*b*) Test plano-spiral, two chambers to a convolution. Genera—*Spiroloculina*, d'Orb. (Fig. 21). All the chambers exposed on the contour. *Biloculina*, d'Orb. (Figs. 22, *a*, and 24). Chambers simple, only the last two chambers exposed on the contour. *Fabularia*, Def. Similar, but chambers subdivided in the interior. *Sigmoilina* (*Planispirina*, pars), Schlumb. (*c*) Three chambers exposed on the contour of the test. Genus—*Triloculina*, d'Orb. (Figs. 22, *b*, and 25). (*d*) Five chambers exposed on the contour of the test. Genus—*Quinqueloculina*, d'Orb. (Fig. 23). (*e*) In the megalospheric form the second chamber completely invests the megalosphere. Genus—*Adelosina*, d'Orb. Chambers arranged on the quinqueloculine plan, or (in *A. polygonia*, Schlumb., Fig 26), plano-spirally, three or four to a convolution. (*f*) Earlier chambers quinqueloculine, later spiroloculine. Genus—*Massilina*, Schl. (*g*) *Miliolinidae trematophorae.* Chambers with inner as well as outer walls, and with sieve-like orifices. Eocene and two recent spp. Genera—*Idalina*, M.-Ch. and Schlumb. Test biloculine in later stages, and ultimately uniloculine; chambers simple (Fig. 27). *Periloculina*, M.-Ch. and Schlumb. Arrangement similar, but chambers partially subdivided by ridges. *Lacazina*, M.-Ch. Uniloculine stage assumed early in growth; chambers subdivided by longitudinal rows of pillars.

FAMILY 2. HAUERINIDAE. First formed part of test milioline or *Cornuspira*-like, later with chambers in spiral or rectilinear arrangement, aperture single. Genera—*Ophthalmidium*, Kübl. Plano-spiral, *Cornuspira*-like at first, later segmented (Fig. 41). *Planispirina*, Seg. Segmented. *Hauerina*, d'Orb. Milioline (? quinqueloculine) at first, then plano-spiral. *Vertebralina*, d'Orb. Plano-spiral at first, then linear. *Articulina*, d'Orb. Milioline (tri- or quinque-loculine) at first, then linear (Fig. 28).

FAMILY 3. PENEROPLIDIDAE. Test plano-spiral, crozier-shaped, or cyclical; usually bilaterally symmetrical; apertures many. Genera—*Peneroplis*, Montfort. Chambers undivided, arranged plano-spirally throughout, or the later ones rectilinear (Fig. 29). *Orbiculina*, Lam. Chambers subdivided by secondary septa; early segments equitant (Figs. 30-32). *Orbitolites*, Lam. Test discoidal, chambers subdivided into chamberlets; early chambers not equitant; arrangement at first plano-spiral, then cyclical (Figs. 33-40). *Meandropsina*, M.-Ch.

FAMILY 4. ALVEOLINIDAE. Test spiral, elongated in the direction of the axis of convolution. Chambers divided into chamberlets. Genus—*Alveolina*, d'Orb. Test subglobular or fusiform.

FAMILY 5. KERAMOSPHAERIDAE. Test spherical, chambers in concentric layers. Genus—*Keramosphaera*, Brady.

FAMILY 6. NUBECULARIDAE. Test irregular, asymmetrical, usually adherent. Genera—*Squamulina*, Schultze. Test a single adherent chamber. *Nubecularia*, Def. Test more or less spiral or adherent, often encrusted with sand.

*Calcituba polymorpha*, Roboz, appears to be a degenerate form of the Miliolidea.

## ORDER 5. **Textularidea.**

Tests of the larger species arenaceous, either with or without a perforated calcareous basis; smaller forms hyaline and conspicuously perforated. Chambers arranged in two or more alternating series, or spiral, or confused; often multiform.

FAMILY 1. TEXTULARIDAE. Typically bi- or tri-serial; often bi-, rarely tri-formed. Genera—*Textularia*, Def. Chambers in two rows, alternating; aperture an arched slit transverse to long axis of test at the base of the inner wall of the final segment. *Cuneolina*, d'Orb. *Verneuilina*, d'Orb. Triserial, with textularian aperture (Fig. 44, C). *Tritaxia*, Reuss. Triserial, with a produced central aperture. *Chrysalidina*, d'Orb. Triserial, with porous aperture. *Bigenerina*, d'Orb. Early chambers textularian, later uniserial (Fig. 44, D). *Pavonina*, d'Orb. Arrangement similar, but test fan-shaped and aperture porous. *Spiroplecta*, Ehrbg. Early chambers plano-spiral, later textularian (Figs. 43 and 44, A-b). *Gaudryina*, d'Orb. Early chambers triserial, later textularian. *Valvulina*, d'Orb. Free or adherent, spiral, typically with three chambers in each convolution. *Clavulina*, d'Orb. Early chambers triserial (valvuline), later uniserial and rectilinear (Fig. 44, E).

FAMILY 2. BULIMINIDAE. Typically spiral; weaker forms more or less regularly biserial, aperture oblique, more or less comma-shaped. Genera—*Bulimina*, d'Orb. Spiral, elongate, more or less tapering, often triserial (Fig. 54). *Virgulina*, d'Orb. Much elongated, often biserial. *Bifarina*, P. and J. Early chambers Bulimine or Virguline, later uniserial. *Bolivina*, d'Orb. Biserial. *Pleurostomella*, Reuss.

FAMILY 3. CASSIDULINIDAE. Test a *Textularia*-like series of alternating chambers, more or less coiled on itself in a plano-spiral manner. Genera—*Cassidulina*, O'Orb. *Ehrenbergia*, Reuss.

### ORDER 6. **Chilostomellidea.**

Test calcareous, finely perforate, polythalamous. Segments following each other from the same end of the long axis, or alternately at the two ends, or in cycles of three; more or less embracing; aperture a curved slit at the end or margin of the final segment. Genera—*Ellipsoidina*, Seg. *Chilostomella*, Reuss. *Allomorphina*, Reuss.

### ORDER 7. **Lagenidea.**

Test calcareous, very finely perforated, monothalamous, or consisting of a number of chambers joined in a straight, curved, spiral, alternating, or (rarely) branching series. Aperture terminal, simple or radiate. No canalicular skeleton or canal system.

FAMILY 1. LAGENIDAE. Test monothalamous. Genus—*Lagena*, Walker and Boys (Fig. 46).

FAMILY 2. NODOSARIIDAE. Test polythalamous, straight, arcuate, or plano-spiral. Genera—*Nodosaria*, Lam. Straight or curved, chambers circular in transverse section, aperture central (Figs. 45, A and B). *Lingulina*, d'Orb. Straight, chambers oval in section, aperture a fissure. *Frondicularia*, Def. Compressed, segments V-shaped (Fig. 45, C). *Rhabdogonium*, Reuss. Straight or curved, triangular or quadrangular in section. *Marginulina*, d'Orb. Elongated, circular in section, aperture marginal. *Vaginulina*, d'Orb. Elongated, septation oblique, aperture marginal. *Rimulina*, d'Orb. *Cristellaria*, Lamk. Plano-spiral in part, or entirely (Fig. 47). *Amphicoryne*, Schlumb. Early chambers cristellarian, later nodosarian. Allied are the fossil biformed genera *Lingulinopis*, Reuss; *Flabellina*, d'Orb.; *Amphimorphina*, Neugeb.; and *Dentalinopsis*, Reuss.

FAMILY 3. POLYMORPHINIDAE. Chambers arranged spirally or irregularly round the long axis, rarely biserial or alternate. Genera—*Polymorphina*, d'Orb. Bi- or tri-serial, or irregularly spiral, aperture radiate (Fig. 48). *Dimorphina*, d'Orb. Early chambers polymorphine, later nodosarian. *Uvigerina*, d'Orb. More or less spiral, aperture produced, often tubular, and lipped. *Sagrina*, P. and J. Early chambers uvigerine, later nodosarian.

FAMILY 4. RAMULINIDAE. Test irregular, branching. Genus—*Ramulina*, R. Jones.

## ORDER 8. **Globigerinidea.**

Test free, calcareous, perforate; chambers few, inflated, arranged spirally; aperture single or multiple, conspicuous. No canalicular skeleton or canal-system. All the larger species pelagic in habit. Genera—*Globigerina*, d'Orb. Test coarsely perforated, trochoid, rotaliform or symmetrically plano-spiral, pelagic specimens usually spinous (Fig. 49). *Orbulina*, d'Orb. A spherical test with large and small perforations, beset with spines, and containing a *Globigerina*-shell. It is a late phase in the life-history of some forms at any rate, of *Globigerina* (Fig. 49). *Hastigerina*, Wy. Th. Regularly nautiloid and involute, armed with long serrate spines, which are triangular in section, aperture large. *Pullenia*, P. and J. Regularly or obliquely nautiloid and involute, chambers only slightly ventricose, aperture a long curved slit, pores very minute. *Sphaeroidina*, d'Orb. Chambers forming together a nearly globular shell. *Candeina*, d'Orb. Trochoid, thin-walled, aperture consisting of rows of pores.

## ORDER 9. **Rotalidea.**

Test calcareous, perforate; free or adherent; typically spiral and "rotaliform," *i.e.* coiled so that all the chambers are visible on the "superior," "dorsal," or "apical" side, those of the last convolution only on the "inferior," "basal," or "apertural side," sometimes one side being convex, sometimes the other. Aberrant forms evolute, outspread, acervuline, or irregular. Some of the higher modifications with double chamber-walls and canalicular skeleton.

FAMILY 1. SPIRILLINIDAE. Test spiral, non-septate. Genus—*Spirillina*, Ehrbg. Complanate and plano-spiral, free or attached.

FAMILY 2. ROTALIDAE. Test rotaliform, rarely evolute, very rarely irregular or acervuline. Genera—*Patellina*, Will. Test conical, with an external layer of spirally arranged or annular chambers, subdivided into chamberlets, the interior of the cone filled either with hyaline shell-substance, or with chambers. *Cymbalopora*, Hag. More or less trochoid. Early chambers spiral, later concentric, pelagic specimens with a large inflated chamber covering the base of the shell. *Discorbina*, P. and J. Free or adherent, rotaliform, trochoid or plano-convex, with either the superior or the inferior (apertural) surface convex, somewhat coarsely porous, aperture an arched slit at umbilical margin of last chamber. *Planorbulina*, d'Orb. Normally adherent, compressed or complanate; chambers very numerous, at first on spiral, later on cyclical plan, and each chamber opening at the periphery; walls coarsely porous. *Truncatulina*, d'Orb. Free or adherent, rotaliform, the inferior face generally more convex than the superior; aperture a curved slit, near the superior (apical) margin of the last chamber. *Anomalina*, P. and J. Like *Truncatulina*, but more nearly plano-spiral. *Carpenteria*, Gray. Adherent, spiral, convex, or monticular; chambers few; aperture at apex of final segment. *Rupertia*, Wallich. Columnar, attached by a spreading base, chambers numerous, spirally arranged, aperture at the basal end of terminal suture of last segment. *Pulvinulina*, P. and J. Rotaliform, finely porous, chambers few, with lines of secondary deposit over the sutures; aperture large, at the umbilical margin of the last segment. *Rotalia*, Lamk. Rotaliform, finely porous, with secondary deposit over sutures or in umbilicus; aperture nearer the peripheral than the umbilical margin of the last chamber; larger spp., with interseptal canals. (Fig. 50.) *Calcarina*, d'Orb. Rotaliform, lenticular, with radiating spines at periphery; canalicular skeleton largely developed.

FAMILY 3. TINOPORIDAE. Test of irregularly massed chambers, the early ones more or less distinctly on a spiral plan; usually without any general aperture. Genera—*Tinoporus*, Carp. Lenticular or subspheroidal, with radiating marginal spines, early chambers arranged in a plano-spiral. *Gypsina*, Carter. Free and spheroidal or attached and spreading, coarsely perforated, no canal-system. *Aphrosina*, Carter. *Polytrema*, Risso. Test usually pink, at first rotaliform and free, then adherent, encrusting or arborescent.

### ORDER 10. **Nummulitidea.**

Test calcareous, finely tubulated, free, spiral, bilaterally symmetrical (except *Amphistegina*), the higher forms with canalicular skeleton and canal system.

FAMILY 1. FUSULINIDAE. Test fusiform or subglobular, chambers extending from pole to pole, each convolution completely enclosing the previous whorls. Genera—*Fusulina*, Fischer. Chambers entire. (Fig. 59.) *Schwagerina*, Möller. Chambers subdivided.

FAMILY 2. POLYSTOMELLIDAE. Test nautiloid. Genera—*Nonionina*, d'Orb. Canalicular skeleton rudimentary or absent, aperture a simple curved slit. *Polystomella*, Lamk. Canalicular skeleton more or less fully developed; aperture a V-shaped line of pores.

FAMILY 3. NUMMULITIDAE. Test lenticular or complanate; a canalicular skeleton and complex canal-system in the higher forms. Genera—*Archaediscus*, Brady. Lenticular, consisting of a non-septate tube irregularly coiled, embedded in finely tubulated envelope. *Amphistegina*, d'Orb. Lenticular, inequilateral, chambers spirally arranged, equitant, the alar prolongations simple on one side of the test, subdivided on the other. *Operculina*, d'Orb. Plano-spiral, the whole of the convolutions exposed; canal-system well developed. (Fig. 55.) *Nummulites*, Lamk. Lenticular or complanate, plano-spiral, regular, chambers equitant their alar prolongations enclosing the previous whorls; a complex canal system. (Figs. 5 and 6.) *Assilina*, d'Orb. Complanate, structure as in *Nummulites*, but the alar prolongation of the chambers are thin, so that the outline of the inner convolutions is visible. *Heterostegina*, d'Orb. Resembles *Operculina* in plan, but the chambers subdivided into chamberlets, and equitant. (Fig. 56.) *Cycloclypeus*, Carp. Chambers usually in a single layer, confined to the median plane of the test; at first spiral, then cyclical (Figs. 57 and 58). *Orbitoides*, d'Orb. Layers of flattened chamberlets are disposed on either side of the chambers of the median plane. Growth probably spiral before it becomes cyclical. *Miogypsina*, Sacco. Early chambers spiral, eccentric.

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# THE PROTOZOA (*continued*)

## SECTION K.—THE SPOROZOA[1]

## CLASS SPOROZOA.

### SUB-CLASS TELOSPORIDIA.

Order 1. **Gregarinida.**
,, 2. **Coccidiidea.**
,, 3. **Haemosporidia.**

### SUB-CLASS NEOSPORIDIA.

Order 4. **Myxosporidia.**
,, 5. **Sarcosporidia.**

### INCERTAE SEDIS.

Order 6. **Haplosporidia.**
,, 7. **Serosporidia.**
,, 8. **Exosporidia.**

INTRODUCTORY.—The Sporozoa are a group of exclusively parasitic Protozoa, of very widespread occurrence, infesting the internal organs or tissues of animals belonging to almost all classes and orders of coelomate Metazoa. There is perhaps no species of annelid, mollusc, arthropod, or vertebrate which is not liable to become the host of some kind of sporozoan parasite, at any rate in certain localities, while many animals harbour several species of these intruders at the same time. Moreover, in some cases, as, for instance, that of the common earthworm, or the mealworm,[2] scarcely an individual can be found which does not contain more or fewer of its particular form of sporozoan parasite. Correlated with their wide distribution, the Sporozoa exhibit the utmost diversity of structural and developmental characters. As a general, though by no means universal, rule, each species of Sporozoön is parasitic on a particular species of host, or on a limited number of allied species, and is usually confined to definite organs or tissues of the host. In other words, the various species of Sporozoa, like most internal parasites, have acquired each an organisation in harmony with certain special conditions of life, and, except for a brief period of their developmental cycle, they cannot exist apart from the very definite and limited environment to which they are exclusively adapted.

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[2] The larva of the meal-beetle, *Tenebrio molitor*.

The Sporozoa also differ widely as regards the effects they produce upon the animals which harbour them. In many, perhaps in most, cases the general health and vital activity of the host seems to be quite unaffected, even when it contains great numbers of the parasites. But in other cases Sporozoa produce dangerous or even fatal diseases, and may be the cause of ravaging epidemics. Instances of this will be found below, especially under the heading of the Myxosporidia. It is sufficient to mention here the various forms of malarial fever in man, now known to be caused by sporozoan parasites of the order Haemosporidia. A still more deadly human disease, namely cancer, has also been referred to the agency of Sporozoa, but this charge has not yet been brought home to them satisfactorily.

Different species of Sporozoa vary between wide limits as regards size, as well as in other characters. From minute organisms, several of which can be contained in a single blood-corpuscle, we find all gradations of size up to creatures whose dimensions must be regarded as very considerable, or even gigantic, in view of the fact that the sporozoan individual is, like other Protozoa, a single nucleated cell. Many of the Gregarines are quite visible to the naked eye, and *Porospora gigantea* (v. Ben.) from the lobster attains a length of 16 mm., or two-thirds of an inch (Fig. 1). In spite, however, of the extremest diversity in size, appearance, organisation, and life-history, the Sporozoa as a group possess certain very characteristic features in common—peculiarities which are clearly in direct relation with their habit of life as internal parasites.

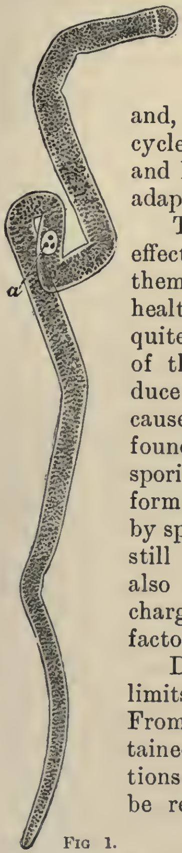

FIG 1.

Trophozoite (sporont) of *Porospora gigantea*, (v. Ben.), × 150. *a*, nucleus. (After van Beneden, from Lankester.)

In the first place, their nutriment is always of a fluid nature, consisting of the juices of the host absorbed osmotically at the surface of the body of the parasite, and none of the special organs for ingesting or digesting solid food, so frequent in other Protozoa, are ever found in this group. Many Sporozoa possess flagella during certain phases of the life-cycle, and many exhibit the power of executing amoeboid movement and emitting pseudopodia during even the whole period of growth; but in both cases the flagella or pseudopodia are organs of locomotion and not of nutrition, except perhaps in so far as the latter may contribute to an increase of the absorptive surface of the body. More usually all such locomotor organs are absent, and the body of the parasite has a fixed form and definite contours, limited externally by a cuticle of greater or less thickness, through which food is absorbed by diffusion. Food-vacuoles or contractile vacuoles are never found.

In the second place, the Sporozoa always possess the power of rapid multiplication by *sporulation* that is to say, by the formation of reproductive bodies or germs, each a fragment of the parent body, in the form of a nucleated protoplasmic corpuscle, usually very minute. These germs may serve for increasing the numbers of the parasite within the same host, or may be the means of disseminating the species and infecting other hosts. In the latter case the germs are usually provided with protective envelopes which enable them to leave the body of the host in which they were produced and to endure for a season the vicissitudes of the outer world. In some cases the protoplasmic germs are naked *gymnospores*, and all those derived from one parent are then enclosed in a resistent *cyst*, formed by the parent previous to sporulation. But in most cases the germs have their own special protective envelopes, and are then termed *chlamydospores*, or more usually *spores* simply. Within the spore-envelope a further multiplication of the germs may take place, and a cyst enclosing all the spores derived from a common parent may or may not be formed. Resistent spores of this kind are one of the most characteristic features of this class, as the name Sporozoa implies. Only in the comparatively small number of cases in which infection is conveyed from one host to another by an intermediate host, are protective envelopes wanting.

The bulk of our knowledge of the Sporozoa is of extremely recent date, and great advances have been made during the last ten years in the investigation of these organisms and the elucidation of obscure points in their life-history. Nevertheless, they did not entirely escape the observation of the earlier naturalists, even so far back as the eighteenth century. As might have been expected, attention was directed first to the larger forms of Gregarines inhabiting Arthropods, especially insects, and later to the characteristic spores, often to be found in vast numbers in various animals.

The first notice of a Gregarine parasite is attributed to the famous anatomist Redi (1708), but his claims to this honour are very doubtful.[1] Cavolini, however, in 1787, described and figured an indubitable Gregarine (*Aggregata conformis* (Dies.), *fide* Labbé) from the glandular appendages of the stomach of *Pachygrapsus marmoratus.* He found conjugating individuals, and believed each such pair to be a kind of tapeworm with two segments. But the true discoverer of the group, in the scientific sense, was Léon Dufour, who, in his researches upon insect-anatomy, became acquainted with, and described, numerous species of these parasites. He regarded them as a peculiar group of worms, allied to Trematodes, to which in 1828 he gave the generic name *Gregarina.* More species were subsequently made known by other authors, and in 1839 Siebold published an important work in which he described the nucleus accurately for the first time, without, however, recognising the true nature of Gregarines, which he also considered as worms, though he did not attribute to them an alimentary canal, as had been done by one of his predecessors! Siebold also described the cysts and spores found associated with the Gregarines, and though he did not discover the connection between them, his observations had the merit of drawing attention to the "pseudonavicellae" already observed by Henle (1835) and others in the sperm-sacs of the earthworm.

Contemporaneously with Siebold's work appeared the investigations of Hake upon the spores of the Coccidium of the rabbit, which, however, the author regarded as pathological products of the tissues of the host itself. In 1841 the celebrated Johannes Müller described the spores of a number of different Myxosporidia inhabiting various fishes, and termed these organisms "psorosperms,"[2] a name of very frequent occurrence in sporozoan literature, applied to various kinds of spores. Müller was, however, quite in the dark as to the nature of his psorosperms, and considered them a "living *seminium morbi*," comparable to spermatozoa. After Müller psorosperms were studied by many observers, and generally divided into "egg-shaped psorosperms," *e.g.* Coccidia, and "fish-psorosperms" or "Müller's psorosperms," the spores of Myxosporidia. Their affinities remained, however, uncertain for a very long time, and indeed the true nature of "fish-psorosperms" has only been elucidated completely in the most recent times. As long ago as 1842 Creplin compared psorosperms to pseudonavicellae, and so laid the foundation of the "Gregarine-theory" of the Myxosporidia. But this comparison was not universally accepted, although supported by Leydig, Lieberkühn, and other observers. Many authors, on the other hand, regarded psorosperms as organisms of a vegetable nature, allied to Diatoms.

A distinct epoch in our knowledge of the Sporozoa was made by Kölliker, who in 1845 and 1848 not only greatly increased our knowledge of these parasites, and of their wide distribution and occurrence in hosts of all classes, but further expressed and maintained for the first time the opinion that Gregarines were unicellular organisms, which should be classed amongst Siebold's Protozoa, and identified Siebold's vesicle as the cell-nucleus. His views were still further borne out by the important observations of Stein, who in 1848 first demonstrated clearly the relation of the pseudonavicellae to the reproduction of the Gregarines, which he placed as a class Symphyta of the Protozoa. The views of Kölliker and Stein have gradually obtained universal assent, especially after the demonstration by Lieberkühn in 1855 of an amoeboid phase in the life-history, and no one now doubts the position of Sporozoa amongst the Protozoa. Nevertheless, for some years this view was energetically combated by various authors, who could not bring themselves to regard the Gregarines as adult, independent organisms. Chief amongst the opponents of the Protozoan theory were Henle, Bruch, and Leydig, who believed that Gregarines were in some way connected with the embryonic stages of Nematodes or threadworms, and more particularly of the genus *Filaria.* In the course of time, and with increase of knowledge, this theory died a natural death, and it became evident that any associations of Gregarines and Nematodes, or resemblances between them, were of a purely accidental and superficial kind. Looking back, however, upon these controversies, now only of historical interest, it is not a little remarkable that in very recent times a curious nematode-like Sporozoön (*Siedleckia nematoides*, Caull. and Mesn.) should have been discovered, which, had it been known in the fifties, might have inclined the balance of zoological opinion strongly over to the side of the Nematode theory.

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[1] See Bütschli, "Sporozoa" in Bronn's *Thierreich*, i. p. 480, from whom most of the historical facts here put together are taken. Labbé [4] identifies the Gregarine figured by Redi as *Aggregata praemorsa* (Dies.).

[2] Derived, according to Balbiani, from ψώρα, mange, and σπέρμα, seed.

A retrospect of the history of our knowledge of Sporozoa further brings into prominence the fact that, as an obscure group of no obvious practical importance, they did not for a long time appeal to the consideration of the "common-sense" Englishman. Until comparatively recent times, practically the only contributions to sporozoan literature in this country were those of Lankester, who, besides other forms, discovered in 1872 the organism, parasitic in the blood of the frog, which at a subsequent date was named by him *Drepanidium ranarum.* This discovery, and that of Laveran, who a few years later made known to science the malarial parasites of human blood, laid the foundations of our knowledge of the Haemosporidia, a group of such importance, from the practical point of view, that they have been the cause of focussing the attention of medical men, no less than of zoologists, in all countries upon the Sporozoa. Indeed, so great is the interest which these parasites excite at the present time, on account of their pathogenic properties in man and beast, that now scarcely a month passes without the publication of some discovery relating to them, and the study of the Sporozoa bids fair to assume in the near future a position of importance scarcely secondary to that held by the science of bacteriology.

*The Structure and Life-history of a Typical Sporozoön.*—As an example of the Sporozoa and of the characteristic features of their life-cycle, we select for detailed description the common *Monocystis agilis*, Stein[1] (Fig. 2), a Gregarine parasitic in the sperm-sacs

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[1] With regard to the proper name of this species, there is a certain amount of confusion and uncertainty, which is none the less regrettable because of so

(vesiculae seminales) of the earthworm (*Lumbricus* spp.). This species is not only very easily obtained, but is also a very typical example of the class; hence in describing the various phases of its life-history it will be possible at the same time to introduce and define the terminology to which we shall adhere in the sequel for the corresponding stages of other Sporozoa. It should be understood, however, that the form which can be selected as most *typical* of a group is not necessarily the most *primitive* of its members. From the type chosen we shall have to work backwards to simpler forms, as well as forwards to more complex.

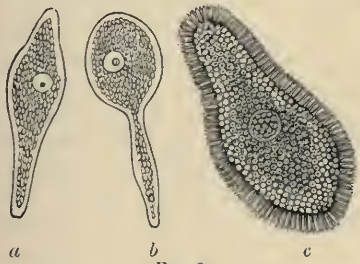

FIG. 2.

Trophozoites of *Monocystis agilis*. *a* and *b*, young individuals showing changes of body-form due to contractility. *c*, an older individual, still enveloped in a coat of spermatozoa. (*a* and *b* after Stein, *c* after Lieberkühn, from Lankester.)

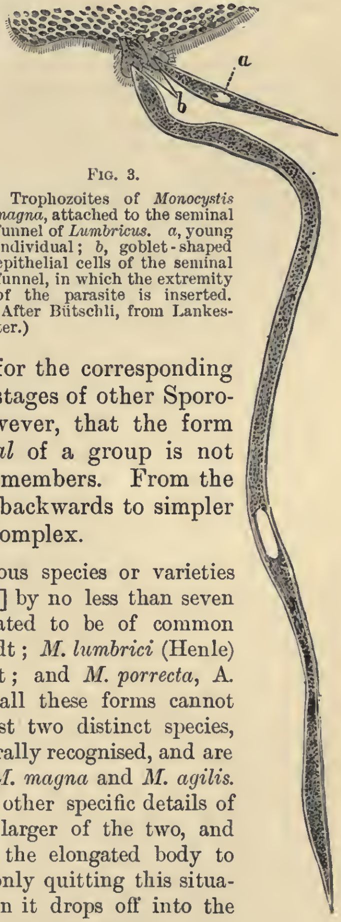

FIG. 3.

Trophozoites of *Monocystis magna*, attached to the seminal funnel of *Lumbricus*. *a*, young individual; *b*, goblet-shaped epithelial cells of the seminal funnel, in which the extremity of the parasite is inserted. (After Bütschli, from Lankester.)

The earthworm is infested by various species or varieties of *Monocystis;* according to Cuénot [13] by no less than seven or eight species, of which four are stated to be of common occurrence, namely, *M. magna*, A. Schmidt; *M. lumbrici* (Henle) (= *M. agilis*, Stein); *M. pilosa*, Cuénot; and *M. porrecta*, A. Schmidt. The specific distinctness of all these forms cannot be unhesitatingly conceded, but at least two distinct species, probably with several varieties, are generally recognised, and are to be found in almost every worm, viz. *M. magna* and *M. agilis.* The two species differ in size and in other specific details of character. *M. magna* (Fig. 3) is the larger of the two, and occurs attached by one extremity of the elongated body to the epithelium of the seminal funnel, only quitting this situation at the period of conjugation, when it drops off into the sperm-sac. *M. agilis* (Fig. 2) is found in the interior of the clumps of developing spermatozoa, or floating freely in the sperm-

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frequent occurrence in the zoological nomenclature of just the commonest or most familiar forms of life, particularly amongst the Sporozoa. According to Labbé [4] the species under consideration should be called *Monocystis tenax* (Dujardin); according to Cuénot [13] its proper designation is *M. lumbrici* (Henle). We refer to these authors for a discussion of these knotty questions, and retain here the name most generally employed, in this country at least, for the species.

sacs. But all essential details of the life-history are quite similar in the two species.

The earliest known stage of *Monocystis agilis* is a minute protoplasmic body, with a distinct nucleus, lodged in one of the "sperm-morulae" floating in the sperm-sac. As is well known, each sperm-morula of the earthworm gives rise to a cluster of spermatozoa, attached by their heads to a central residual mass of protoplasm termed the "sporophore." The young *Monocystis* is found within the sporophore and grows at its expense and at that of the attached spermatozoa. This stage of the parasite, during which it is absorbing nutriment from its host and growing rapidly, may be termed the *trophic stage*, and each individual parasite during this stage may be termed a *trophozoite.* The parasite soon becomes elongated in one direction. It assumes first an oval contour and becomes later more or less vermiform. As it grows it destroys the sperm-cluster in which it is lodged, and in later stages it is found enveloped in an adventitious coat or fur composed of the tails of the degenerated spermatozoa, giving the appearance of a ciliated covering, which is thrown off in the final stages of growth (Figs. 2, *c*, and 4, *a*).

The full-grown trophozoite (Fig. 2) is still a single cell, with a single nucleus. The body is limited by a distinct cuticle, within which the protoplasm is differentiated into an external clear cortical layer or *ectoplasm*, and an internal granular medullary layer or *endoplasm.* The ectoplasm is the seat of contractility, and contains in its deepest part a layer of fine contractile fibres, the so-called *myocyte-fibrillae.* The endoplasm lodges the nucleus, and contains numerous coarse granules representing nutriment held in reserve for impending reproductive and developmental processes. The nucleus is a clear spherical body, in the form of a vesicle limited by a delicate membrane, containing fluid in which float one or more nuclear corpuscles or *karyosomes.* Each karyosome is a small globule, resembling in appearance the nucleolus of a tissue-cell, but differing from it in containing a certain amount of chromatin in its substance. The karyosomes usually have a vacuolated structure. The trophozoite is actively motile, as the specific name implies. In *Monocystis* the movements consist chiefly of changes of form brought about by the contractility of the myocyte-fibrillae, whereby the body may be bent or contracted as a whole, or may exhibit ring-like constrictions in different parts.

After the trophic stage, which is a period of purely vegetative growth, the parasite enters upon the reproductive phase of its life-history, a period in which two distinct events follow each other; first, the formation of *gametes* or conjugating individuals, which pair with one another and unite to form *zygotes;* secondly, the formation from the zygotes of the resistent spores, by which the parasite is disseminated (see Fig. 29, p. 185).

The adult trophozoite, when it is ripe for reproduction, is commonly known as a *sporont*, but may be better termed a *gametocyte*, since it gives rise to the gametes. Two gametocytes come together and become very closely apposed to form a spherical body (Fig. 4), the two individuals remaining, however, perfectly distinct from one another, each forming one hemisphere of the common mass. This union of the two gametocytes must not be confounded with the true conjugation: the two individuals are merely in association; they are keeping company, as it were, as a preliminary to the formation of gametes. The two associated gametocytes, which often exhibit a slow rotatory movement, now become surrounded by a common envelope or *cyst* (Fig. 4, *b*, *c.m*), secreted by them in two layers; first a rigid external *epicyst*, then a thin internal *endocyst*.[1] Meanwhile important changes are going

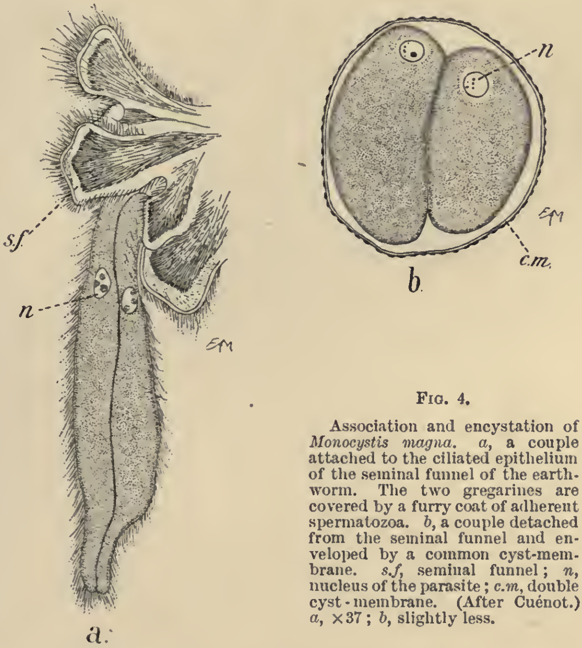

FIG. 4.

Association and encystation of *Monocystis magna*. *a*, a couple attached to the ciliated epithelium of the seminal funnel of the earthworm. The two gregarines are covered by a furry coat of adherent spermatozoa. *b*, a couple detached from the seminal funnel and enveloped by a common cyst-membrane. *s.f*, seminal funnel; *n*, nucleus of the parasite; *c.m*, double cyst-membrane. (After Cuénot.) *a*, ×37; *b*, slightly less.

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[1] According to Cecconi [11], in *M. agilis* the sporonts first become encysted singly, and two such cysts then approach each other and join together. This probably applies only to the first signs of cyst-formation, as two completely encysted gregarines can hardly be sufficiently motile to admit of their travelling towards one another.

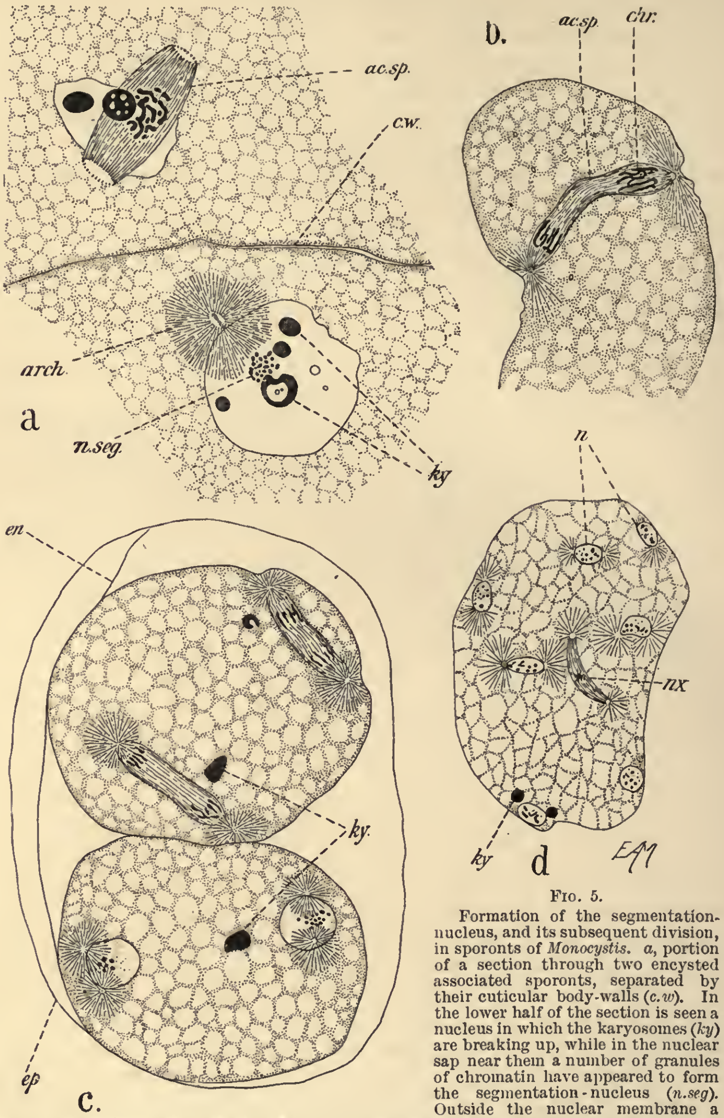

FIG. 5.

Formation of the segmentation-nucleus, and its subsequent division, in sporonts of *Monocystis*. *a*, portion of a section through two encysted associated sporonts, separated by their cuticular body-walls (*c.w*). In the lower half of the section is seen a nucleus in which the karyosomes (*ky*) are breaking up, while in the nuclear sap near them a number of granules of chromatin have appeared to form the segmentation-nucleus (*n.seg*). Outside the nuclear membrane a patch of archoplasm (*arch*) has appeared. In the upper half the archoplasm has divided to form an achromatic spindle (*ac.sp*), in the middle of which are seen the chromatin granules of the segmentation-nucleus; two karyosomes are also seen, one showing a vacuolated structure. *b*, section through one sporont of an associated couple in a cyst, showing the segmentation-nucleus in the diaster stage. The karyokinetic spindle (*ac.sp*) stretches across the whole body. The chromosomes (*chr*) form two groups. *c*, section through a couple of encysted sporonts, showing in the lower one two resting nuclei preparing for division, and the remains of a karyosome in the cytoplasm; in the upper one two nuclei in the diaster stage, and two karyosomes; *ep*, epicyst; *en*, endocyst. *d*, section through one sporont of a couple showing seven resting nuclei (*n*), one dividing nucleus (*nx*), and two karyosomes (*ky*). (After Cuénot.) *a*, × 1180; *b* and *d*, × 560; *c*, × 790.

on within the bodies of the gametocytes. In the nucleus of each individual the karyosomes break up and become partially dissolved in the nuclear sap (Fig. 5, *a-d*, *ky*). At the same time a number of chromosomes, in the form of grains or short filaments of chromatin, appear grouped in a clump in the nuclear sap,[1] constituting a renovated chromatic nucleus which may be termed the segmentation-nucleus (Fig. 5, *a*, *n.seg*). At this point the nuclear membrane disappears and the segmentation-nucleus divides by karyokinesis, forming a nuclear spindle which becomes elongated until it stretches across the whole body of the gametocyte (Fig. 5, *a* and *b*, *ac.sp*). The two daughter-nuclei divide again in their turn, and in this way repeated nuclear divisions follow one another in each gametocyte; but those in one individual take place independently of those in the other, and are not synchronous (Fig. 5, *c*). The karyosomes of the primitive nucleus are left free in the cytoplasm and are slowly absorbed. As the nuclei multiply, their size, and that of the karyokinetic spindles, diminishes until it reaches a minimum (Fig. 5, *b* and *d*). Nuclear division then ceases, and the minute nuclei travel to the surface of the body. The cytoplasm of the gametocyte now breaks up into a number of small masses each centred round one of the tiny nuclei. Each of the small nucleated bodies thus formed is commonly termed a sporoblast, but should be distinguished as a primary sporoblast, or better still, as a *gamete* (Fig. 6, *a*). The protoplasm of the gametocyte is not entirely used up to form the gametes, but a surplus of residual protoplasm is left over, termed the *cystal residuum* ("reliquat kystal," "Restkörper"), which serves for the nutrition of the sporoblasts during their further development. In the residuum are found also a certain number of degenerated nuclei (Fig. 6, *r.p*, *r.n*).

The next step is the conjugation of the gametes, which takes place within the cyst. The cuticle which formed primitively the body-wall of each gametocyte becomes dissolved, and the two original individuals can no longer be distinguished, since the gametes and other protoplasmic fragments derived from them become intermingled. The gametes themselves now begin to exhibit lively movements, the so-called "dance of the sporoblasts," which gradually cease as they conjugate in pairs. It is probable that in each pair one gamete is derived from one of the two parent gametocytes, and the other from the other, but it is by no means certain that this is always the case. The two conjugating gametes unite completely to form a single *zygote* or *definitive sporoblast*, in which the two nuclei also fuse, the grains of chromatin being intermingled, but retaining their distinctness (Fig. 6, *b*, $z^1$-$z^3$).

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[1] According to Cuénot the chromosomes are formed independently of the karyosomes, but it is more probable that, as in Coccidia (p. 216), their chromatin substance is derived from a part of that which is stored up in the latter. The more recent observations of Prowazek [25*a*] confirm this supposition.

Each sporoblast now becomes a *spore* in the following way. The sporoblast becomes of oval form and secretes on its surface a tough membrane or *sporocyst*, of a substance resembling chitin (Fig. 6, *c*, Fig. 7, *A*, *B*). Within the sporocyst the nucleus of the sporoblast, or, as it may now be termed, the *sporoplasm*, divides into two, then into four, and finally into eight nuclei, by three successive amitotic divisions. The eight nuclei take up an equatorial position, and round each one some of the protoplasm of the spore becomes aggregated, and segmented off as a minute sickle-shaped germ (Fig. 7, *C*) termed a *sporozoite*

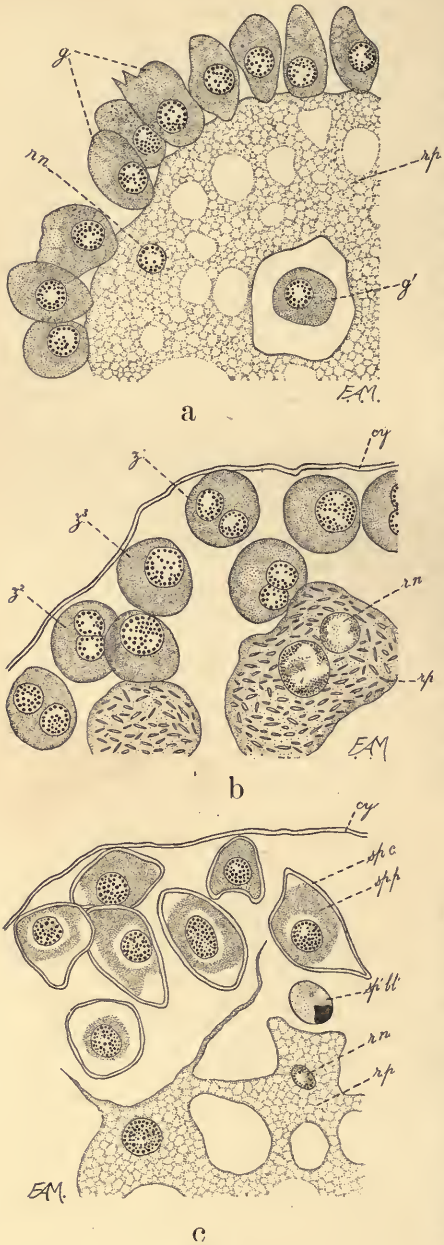

FIG. 6.

FIG. 6.

Formation of gametes (primary sporoblasts) and their conjugation in *Monocystis*, seen in sections. *a*, portion of a section through a sporont showing the gametes (*g*) formed at the periphery of the body round the residual protoplasm (*r.p*). Occasionally a gamete (*g'*) may be formed deep in the residual protoplasm, which contains also residual nuclei (*r.n*). *b*, the gametes have fused in pairs to form zygotes, in all of which the fusion of the cytoplasm is complete, but the nuclei are either still separate ($z^1$) or beginning to unite ($z^2$) or completely fused ($z^3$). The residual protoplasm (*r.p*) is breaking up into separate masses, in some of which degenerating residual nuclei (*r.n*) are to be found; *cy*, cyst-envelope. *c*, the zygotes (definitive sporoblasts) have begun to secrete sporocysts (*sp.c*), within which the sporoplasm (*sp.p*) is becoming contracted; a few sporoblasts degenerate (*sp'.bl'*). Other letters as before. (After Cuénot.) × 1180.

("falciform body," "Sichelkeim"). The protoplasm of the sporozoites is finely granular, and when they are formed, a surplus of coarsely granular protoplasm is left over from the sporoplasm as the *sporal residuum* ("reliquat sporal"). The fully-formed spore has in *Monocystis* the form shown in Fig. 7, *C*; it is more or less boat-shaped, and resembles a diatom of the genus *Navicella*, whence is derived the name *pseudonavicella*, by which Gregarine spores have long been known. The sporocyst is slightly thickened at each pole, and within this very resistent and impervious envelope the eight sporozoites are packed lengthways round the centrally placed sporal residuum. During the formation of the spores the cystal residuum is slowly absorbed, and the ripe cyst contains only a great number of the pseudonavicellae, not arranged in any definite pattern (Fig. 8).

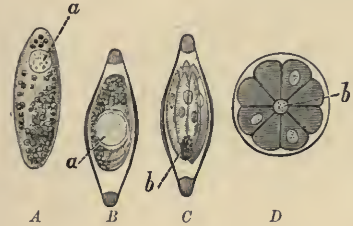

FIG. 7.

Development of the spore of *Monocystis*. *A*, oval sporoblast with single nucleus (*a*). *B*, the sporoblast has secreted the sporocyst at its surface, and the sporoplasm within it has become contracted and diminished in volume. *C*, ripe spore with eight sporozoites and residual protoplasm (*b*). *D*, diagrammatic cross-section to show the arrangement of the sporozoites round the central residual protoplasm. (After Bütschli, from Lankester.)

The above account of the conjugation and spore-formation is that given recently by Cuénot, whose researches confirm the discoveries of Siedlecki with regard to an allied form *Lankesteria ascidiae* (Lank.), and are in harmony with the still more recent account given by Leger [23] for *Stylorhynchus*. Cuénot's description of the spore-formation and the events antecedent to it is confirmed in all essential details by Cecconi [11] and Prowazek [25*a*]. Previous to Cuénot the reproduction of *Monocystis* had only been studied by Wolters [29], whose description of the process is very different. According to Wolters the association of the two full-grown trophozoites or sporonts within the cyst is a true conjugation, similar in its details to that known in *Actinophrys* from the researches of Schaudinn. Wolters describes the nucleus of each sporont as dividing mitotically to form two nuclei, one of which is given off in a polar body, while the other remains as a pronucleus. The two nuclei are then stated to travel towards the septum formed by the apposition of the cuticular body-walls of the two sporonts, and at one point the septum becomes dissolved, permitting the fusion of the pronuclei into a single nucleus. After a time the fusion-nucleus divides into two nuclei, which then rapidly divide up to form numerous small nuclei, round which the protoplasm of the sporonts becomes segmented to form the sporoblasts. From the sporoblasts the spores are formed as above described.

It is unfortunate that these statements of Wolters, which seem to be totally erroneous, have remained uncontradicted for ten years, during which time they have got into numerous text-books and have been generally accepted and taught.

The spores of *Monocystis* do not appear to be able to develop further in the earthworm, but require to be transferred to a fresh host before they can germinate. How the infection is effected has not yet been ascertained in the case of the type that has been selected for description, and the course of events can only be conjectured by analogy from what is known to take place in other Sporozoa. It is highly probable that the spores pass to the exterior and are scattered broadcast in the earth, and that they are then swallowed accidentally by an earthworm with its food, and so pass into its digestive tract. The action of the digestive juices upon the spores has the effect of causing the sporocysts to burst open, setting free the sporozoites, which are actively motile and possess the power of boring their way through cells and tissues. In this way the sporozoites probably traverse the wall of the earthworm's intestine and reach the reproductive organs, where each one attacks a sperm-mother-cell

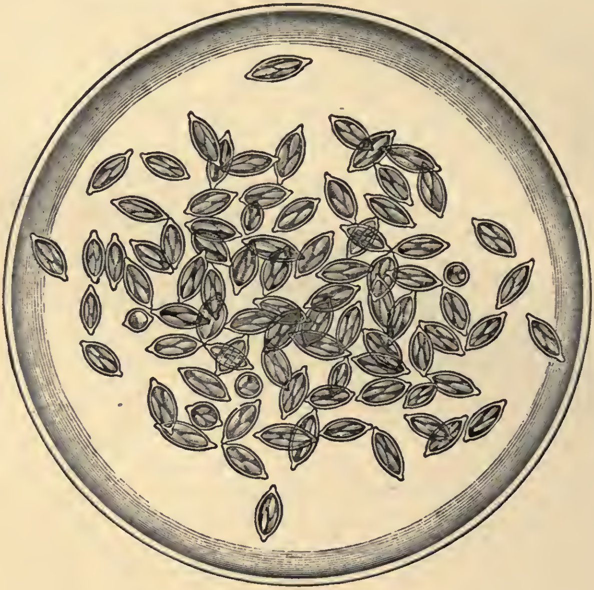

FIG. 8.

Ripe cyst of *Monocystis*, showing the numerous spores (pseudonavicellae) scattered within the cyst, without any cystal residuum present. (From Lankester.)

and there develops into the minute trophozoite which is formed later within the sperm-morula. With this stage the life-cycle has come round again to the point at which the description of it was commenced.

A few points with regard to the life-cycle require brief further discussion. It has been suggested that the spores may sometimes germinate in the host in which they are formed, and so increase the numbers of the parasite within it. But the improbability of this occurring is very great, as was pointed out by Bütschli, in view of the relatively small number of parasites in the trophic stage which are met with, as compared with the vast number of spores. Thus in a given earthworm there will be found in the sperm-sacs perhaps a dozen trophozoites and as many ripe cysts. Each of the latter contains, however, at a low estimate about fifty spores, and each spore eight sporozoites. A single cyst contains, therefore, about four hundred individuals, more or less, and if it were a frequent occurrence for the spores to germinate in the same host, the number of trophozoites in each earthworm might be expected to be vastly greater than is usually the case.

Another question which may be raised is whether the *Monocystis* has any method of multiplication during the trophic phase, that is to say, in the period from sporozoite to sporont. It has sometimes been stated that the trophozoites multiply by division during the earlier stages of growth. From what is known of other Sporozoa, there is nothing inherently improbable in this view, but it has not been proved satisfactorily that such multiplication can take place in *Monocystis*, and the abovementioned paucity of the trophozoites is an argument against its occurrence.

With regard to the passage of the spores to the exterior, precise information is lacking as to how this is effected. In Sporozoa generally we find one of two conditions. In some cases the spores are produced in a position where they can leave the body by natural channels, as in the numerous instances of sporozoan parasites lodged in the digestive tract, when the cysts and spores are cast out with the faeces. In other cases the spores cannot pass out by natural channels, and are set free either by provoking suppuration or other organic disturbance, or by the death and break-up of the host. In the case of the *Monocystis* of the earthworm, the spores could only be discharged from the body, in the ordinary course of events, by passing out of the sperm-sac with the sperm at copulation. They would then be transferred to the spermathecae or receptacula seminis of another worm, and would pass ultimately into the cocoon in which the eggs are laid; but there is no record of their occurrence in either of these situations. It seems more probable that spores are set free by the dissolution of their host. Very possibly birds or some other of the numerous creatures which prey upon worms are the agents by which the dissemination is effected. If a bird swallowed an earthworm containing spores of *Monocystis*, from which very few worms are free, the spores would probably pass unaltered thorough the bird's digestive tract. Uninjured spores of Gregarines have been observed by

L. Pfeiffer in the intestines and faeces of various birds.[1] A parallel case is that of the *Coccidium* infecting the centipede *Lithobius*, the spores of which, if swallowed by another animal, such as a wood-louse, pass unaltered through it (see p. 221). If this suggestion be correct, it is easy to understand that any worm-eating bird would be continually scattering spores of *Monocystis* on the ground, where they would wash down into the soil and be swallowed very easily by worms again. There is, however, no direct evidence bearing upon the mode of dissemination of the spores, and the above suggestion must be regarded merely as a more or less probable surmise.

When the spores have reached the digestive tract of their new host, and the sporozoites have been liberated there, the question arises how they reach the sperm-sacs. This problem, however difficult to solve, is by no means one peculiar to the *Monocystis* of the earthworm. In many other Sporozoa we have instances of parasites affecting some particular organ, which invade the body in the first place from the digestive tract. It must be assumed that the sporozoites have in some way the power of selecting the particular organ they affect, and of migrating through the body of the host in order to reach their specific habitat. Probably they make use of vascular or lymphatic channels in order to arrive at their destination.

*General Characters of the Sporozoa.*—From the above account of *Monocystis* it is seen that the life-history of a typical Sporozoön is a single cycle, which may be summed up in the following way :[2]—

$$\left.\begin{array}{l}\text{Sporozoite}\rightarrow\text{Trophozoite}\rightarrow\text{Gametocyte (Sporont)}\times n\text{ Gametes}\\ \text{Sporozoite}\rightarrow\text{Trophozoite}\rightarrow\text{Gametocyte (Sporont)}\times n\text{ Gametes}\end{array}\right\}+$$
$$=n\text{ Zygotes (Sporoblasts)}\rightarrow n\text{ Spores}\times 8n\text{ Sporozoites.}$$

The life-cycle may further be divided into three main periods.

First, the period of growth, during which the minute sporozoite grows by absorption of nutriment from the host into the sporont.

Secondly, the period of proliferation, accompanied by conjugation, and resulting in the formation of a large number of germs, destined to spread the species.

Thirdly, the period of rest, during which the parasitic germs pass out from the host into the outer world, to effect, if fortune favour them, the passive infection of a new host.

In Sporozoa, considered generally, the life-history is similar in the main to that described above, but exhibits, in different forms, variations of every kind, in the direction either of greater or of less complexity. The deviations from the selected type may be considered from two points of view, according as they affect the characters (I.) of the individual stages or (II.) of the whole life-cycle.

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[1] *Fide* Wasielewski [7], p. 26.

[2] In this and in all subsequent formulae of sporozoan life-histories an arrow is used to mean "becomes" or "grows into"; the sign × to indicate a distinct cell-generation, a multiplication of individuals of any kind; and a bracket with the sign + to denote the occurrence of zygosis or true conjugation and fusion of gametes.

I. Each phase of the life-history may be varied or modified in structural or other details, in accordance with the special environment and conditions of life to which a given species of these parasites is adapted. The modifications that occur under this head will receive detailed treatment in due course in the systematic review of the orders, families, and genera of Sporozoa in the sequel, but a few of the more important variations and simplifications may be considered here. The trophozoites have commonly, as in *Monocystis*, a definite body-form, limited by a cuticle; but in many forms the protoplasm is naked, and the body is amoeboid, and of indefinite and changeable form. In *Monocystis* the gametes are not differentiated and the conjugation is *isogamous*, but in other types there may be *anisogamous* conjugation between sharply differentiated male and female gametes. The greatest variation, however, is seen in the spores. The number of the sporozoites is usually eight in Gregarines, but may be greater or less in other types. Hence the spores are distinguished as *monozoic*, *dizoic*, *tetrazoic*, *polyzoic*, and so forth, according as they contain one, two, four, or many sporozoites. In the monozoic condition there is no secondary multiplication within the sporocyst, but each sporoblast simply becomes a sporozoite. In many such cases the sporoblast secretes no sporocyst, but becomes a naked *gymnospore*, resembling a free sporozoite. These gymnospores may be formed within a resistent cyst secreted round the sporonts, or the cyst may be entirely absent. And further, the spore-formation may be preceded by conjugation of gametes, or the spores may be produced asexually, by the segmentation of a single sporont.

Hence in an ideally primitive type of sporozoan development, the full-grown trophozoite or sporont simply breaks up, without previous conjugation or encystment, into a number of naked gymnospores, and each of them becomes a trophozoite which is similar to its parent, and repeats the process in due course.

II. The plan and character of the life-cycle as a whole may be greatly varied, and secondary modifications or complications of various kinds introduced into it. The more important of these variations will be briefly described.

(1) In *Monocystis* it has been seen that the period of growth and the period of proliferation are sharply separated, the latter following upon the former. The same is the case in the whole order Gregarinida, to which *Monocystis* belongs, and also in two other orders, the Coccidiidea and the Haemosporidia. On the other hand, in the two orders known as Myxosporidia and Sarcosporidia, spore-formation commences at an early stage in the growth of the

trophozoite, and spores are formed continually during the trophic stage, so that there is no distinction between trophozoite and sporont. Hence it has been proposed by Schaudinn to group the Gregarinida, Coccidiidea, and Haemosporidia together as a sub-class *Telosporidia*, contrasting them with a sub-class *Neosporidia* comprising the Myxosporidia and Sarcosporidia. The Telosporidia are Sporozoa in which the reproductive phases follow completion and cessation of growth; the Neosporidia are Sporozoa in which growth and reproduction go on at the same time. It is probable that this distinction indicates the deepest phylogenetic cleft in this class of Protozoa.

(2) In *Monocystis* the whole life-history is a single cycle, adapted entirely to spreading the infection amongst new hosts; it is, in fact, *monogenetic*. But in many other Sporozoa, belonging to either of the two sub-classes recognised above, the parasite may be capable of rapid multiplication within the body of its host, which it thus completely overruns in many instances. In such cases the life-cycle becomes *digenetic*, that is to say, it is differentiated into two distinct generations or series of generations, the one *endogenous* or self-infective, the other *exogenous* or cross-infective. In the endogenous generations the reproductive processes are usually of a primitive type, taking place by binary or multiple fission, or by a simple form of sporulation, known as *schizogony*, in which a trophozoite, without encystation, breaks up into numerous gymnospores, implanted on a certain amount of residual protoplasm. The sporulating individuals in this case are termed *schizonts*, and the gymnospores are known as *merozoites*, to distinguish them from the sporozoites of the exogenous generation. After a number of endogenous generations, the parasite soon or later reproduces itself by exogenous generation or *sporogony*, with the formation from sporonts of resistent spores that can be disseminated outside the body of the host. In monogenetic types the life-cycle consists of sporogony alone.

(3) Considerable differences are seen in the manner in which the infection of a new host is brought about. The vast majority of Sporozoa appear to be disseminated passively, and the spores are taken up directly, in an accidental manner, by another host of the same kind as that from which they came. Should the spores chance to be devoured by an animal of another species, they will either be digested completely or will pass through its body unaltered. Only in their proper host do the digestive juices have the effect of liberating the sporozoites without harming them. In some cases, however, especially amongst Sporozoa parasitic in the blood, an intermediate host has been acquired, and is the agent by which the parasite is disseminated. The best-known instance of this is found in the malarial parasites, and is fully described

below. Here the endogenous generations multiply by schizogony in the blood of a vertebrate host, until sporonts are formed, which must be taken up by a blood-sucking insect, such as a mosquito, in order to develop further. In the invertebrate host the exogenous generation takes place, and the sporonts give rise, by sporogony after conjugation, to a number of gymnospores or sporozoites, with which the vertebrate host is again inoculated.

In Sporozoa up to the present three modes of infection have been observed. The first and commonest method may be termed *casual* infection, where there is no intermediate host, and the infection is acquired by swallowing spores accidentally with the food. In the malarial parasites the infection is effected by the *inoculative* method, through the agency of an intermediate host. The third method is that of *hereditary* infection, a rare type, but known in at least one instance, the silkworm-disease produced by the myxosporidian parasite *Glugea bombycis* (see p. 290), and possibly occurring also in the tick-fever parasites of cattle and other mammals (p. 262). In the first of these two instances the parasites penetrate the ovum and produce spores there, which germinate and infect the next generation of the host. It is possible that to these three modes a fourth should be added, which may be termed the *contagious* method, seen in the parasites which cause certain human skin-diseases (p. 238), but the sporozoan nature of these bodies is by no means demonstrated with certainty.

*Classification of the Sporozoa.*—At least five well-established orders of Sporozoa are generally recognised—the Gregarinida, Coccidiidea, Haemosporidia, Myxosporidia, and Sarcosporidia. In addition, there are three orders which are at present less well known and of very uncertain value—the Haplosporidia, Serosporidia, and Exosporidia. The organisms formerly known as Amoebosporidia must now be included in the Gregarinida.

Many ways of grouping these orders into higher subdivisions or subclasses of the Sporozoa have been proposed. Labbé set up two subclasses: (1) Cytosporidia, in which the trophozoite is intracellular, either throughout the trophic period or at least in the earlier stages of growth; (2) Histosporidia, in which the trophozoite is an intercellular tissue-parasite. The Cytosporidia comprise the Gregarinida, Coccidiidea, and Haemosporidia; the Histosporidia include the Myxosporidia and Sarcosporidia. The grouping proposed is a natural one, but the distinctions on which Labbé founded it have not the value which he attributed to them, since the young stages of the Histosporidia are intracellular as often as they are intercellular. Labbé now [4] subdivides the class into Cytosporidia, defined as having "no spore, or a simple spore without polar capsules," and Myxosporidia, having "the spore furnished with polar capsules containing an evaginable filament," while the Sarcosporidia are relegated to the Sporozoa incertae sedis.

Delage and Hérouard [2] in their classification made use of the character of the sporozoite or protoplasmic germ within the spore, and divided the class into (1) Rhabdogeniae, "with sporozoite of definite form, generally falciform (arquée)" (Gregarinida, Coccidiidea, Haemosporidia, and Sarcosporidia); and (2) Amoebogeniae, "with amoeboid sporozoite" (Myxosporidia). This classification has the disadvantage, however, of separating the two nearly allied groups Myxosporidia and Sarcosporidia, and it has not been followed by any subsequent writers.

Mesnil [6], making use of names invented by Metschnikoff, divides the Sporozoa into Ectospora (Gregarinida, Coccidiidea, and Haemosporidia) and Endospora (Myxosporidia, Sarcosporidia, and Haplosporidia). In the Ectospora, the sporulation takes place at the close of the trophic period, and the spore-mother-cells (sporoblasts) are formed at the periphery of the sporont; in the Endospora, spore-formation goes on during the growth of the trophozoite, and the spore-mother-cells (pansporoblasts) are cut off in the interior of the body (p. 283).

In the sequel the classification of Schaudinn into two groups, Telosporidia and Neosporidia, as defined above (p. 166), is followed. It is seen that, as compared with the classifications of Labbé and Mesnil, the distinction depends rather on the mode of defining the two subdivisions than on essential differences in the plan of grouping the orders.

# SYSTEMATIC REVIEW OF THE SPOROZOA

## SUB-CLASS TELOSPORIDIA.

*Sporozoa in which the reproductive phase of the life-cycle is distinct from, and follows after, the trophic phase.*

### ORDER 1. **Gregarinida.**

The Gregarinida, commonly known as Gregarines, are an order of the Sporozoa remarkable for the degree to which structural complexity of the individual, and adaptive specialisation of the species, are carried. On the other hand, the life-cycle is usually extremely simple. It might, in fact, be said, speaking generally, that the Gregarines are the highest of the Sporozoa from the standpoint of morphology, and the most differentiated from the point of view of taxonomy, but are at the same time amongst the simplest as regards reproductive phenomena. Their distinctive characters are as follows:—The trophozoite commences its growth typically as an intracellular parasite, usually, if not always, of an epithelial cell; never of a blood-corpuscle. It soon outgrows the host-cell, and bulges from it, and finally drops out into an internal cavity of the host, usually the digestive tract, but often the haemocoele (blood-vessels or body-cavity), and sometimes the true coelom. Here it continues to grow, absorbing nutriment from its host, until it becomes a ripe, full-fed sporont. It then encysts, with or without previous association with another of its kind, and the process of spore-formation or sporogony commences. Sporoblasts are formed which usually secrete sporocysts and give rise to spores, and within the spore-envelope the sporoplasm breaks up into sporozoites, eight in number as a general rule. In a few rare instances there is endogenous reproduction by schizogony, in addition to the ordinary sporogony.

As has been said above, the Gregarines were the earliest Sporozoa to be observed and studied, on account of their large and conspicuous size. The history of the group may be said to commence, for all practical purposes, with the founding of the genus Gregarina by Dufour in 1828. From that time onwards numerous observers, amongst whom Aimé Schneider and Léger deserve special mention, have added to our knowledge of the abundance of genera and species of these parasites, or have studied the details of their life-history and development. Nevertheless, it is only in the most recent times, practically in the new-born twentieth century, that the facts concerning the conjugative processes have become accurately known, largely in consequence of renewed investigations upon them stimulated by the interesting discoveries made in other orders of Sporozoa.

*Occurrence, Habitat, etc.*—The Gregarines are confined for the most part to invertebrate hosts, and have never yet been found in any craniate vertebrate. The great majority of them lead blameless lives in the interiors of various arthropods, to which the segmented forms comprised in the sub-order Cephalina are almost confined. The unsegmented forms are found commonly, however, in other groups also, especially in echinoderms, in annelids, including gephyrea and hirudinea, and in tunicata. A few have been recorded from turbellaria, nemertines, and enteropneusta, and a doubtful species is known from Amphioxus. In molluscs, however, they are almost unknown, the single recorded instance being a species from the body-cavity of *Pterotrachea.* Thus the Gregarines are to a large extent the opposite to the Coccidia in the matter of the hosts they affect, the arthropods alone being ground common to the two orders.

The infection of the host is probably effected in all cases by way of the digestive tract, and the sporozoites, when liberated there, proceed to attack the lining epithelium. In some cases the sporozoite traverses the epithelium without stopping, passing on into the haemocoele, as in *Diplocystis* of the cricket, or into the coelom or one of its subdivisions, as in *Monocystis.* In other cases it remains attached to an epithelial cell only by a small portion of the body; the intracellular stage or "Coccidian phase" being practically suppressed. In other cases, again, a large portion of the body, containing the nucleus, is imbedded in the epithelial cell, while the rest of the body projects freely from the host-cell. But in typical cases the youngest trophozoites are found as intracellular parasites, completely enclosed by a cell of the epithelium, either of the gut or some of its diverticula. In this situation the parasite grows rapidly, and soon becomes larger than the host-cell. The trophozoite then falls out of the exhausted cell, usually passing inwards towards the lumen of the gut, sometimes, however, outwards into the vascular system or body-cavity. Gregarines in the latter situation are commonly termed "coelomic," without distinguishing whether the body-cavity in which they lie is a true coelomic space or a part of the haemocoele. Coelomic Gregarines, in the latter sense, occur very frequently in insects (Fig. 9), and in many cases a Gregarine may occupy different situations at different periods of the life of its host. It commonly happens that a Gregarine inhabiting the digestive tract of an insect-larva passes through the wall of the gut at the metamorphosis, and so becomes a coelomic Gregarine in the imago.

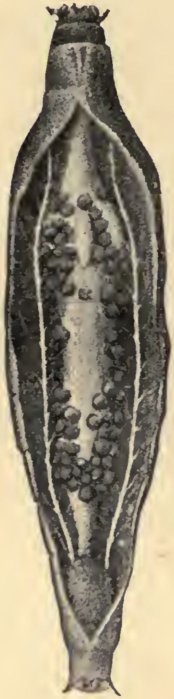

Fig. 9.

Larva of *Tipula oleracea*, opened to show the gut covered with coelomic Gregarine cysts. (From Wasielewski, after Léger.)

The young trophozoites have been shown to have remarkable effects upon the cells in which they are parasitic. The infected host-cell passes through two successive phases — first one of hypertrophy, then of atrophy. The facts have been investigated by Laveran and Mesnil [16], and still more recently by Siedlecki [28], in several species. The youngest trophozoites of *Lankesteria ascidiae*, studied by Siedlecki, place themselves deep in the basal portion of the epithelial cell, the region where the protoplasm of the cell is least differentiated for secretion (Fig. 10, *a*). The nucleus of the host-cell soon begins to appear swollen, its chromatin network becomes loose and stains in a diffuse manner, and its nucleolus increases greatly beyond the normal size, acquiring irregular contours and often dividing into several parts. Hypertrophy of the nucleus is soon followed by that of the cytoplasm, which appears clearer than in the adjacent cells, apparently as the result of a sort of liquefaction. The protoplasm becomes difficult to fix, and always stains much more feebly than the protoplasm of neighbouring cells. The Gregarine meanwhile is also increasing in size, and its rate of growth exceeds that of the infected cell. When it is large enough to fill the hypertrophied host-cell, degeneration of the latter commences (Fig. 10, *b*). Its nucleus shrinks, becomes crescent-shaped, and finally becomes a flattened corpuscle which stains strongly and consists of débris of chromatin. At the same time the cytoplasm is absorbed until it forms a thin skin enclosing the Gregarine, and is finally cast off with it from the epithelium. It is remarkable that in other cases a similar series of changes may be provoked in the epithelial cell after the Gregarine has grown out from it, and is attached to the cell only by a minute point of contact (Fig. 11).

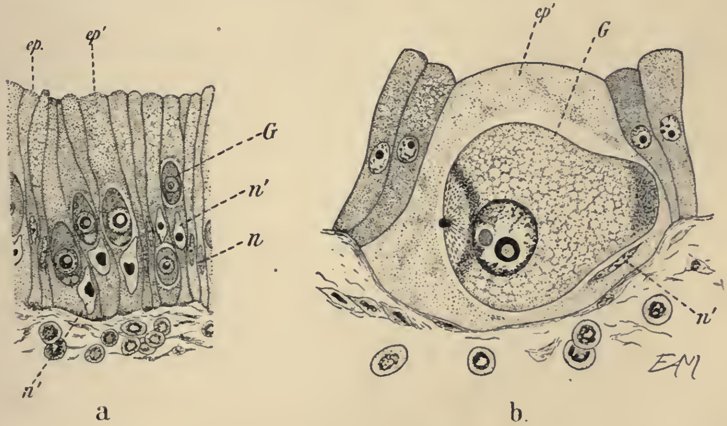

Fig. 10.

Intracellular stages of *Lankesteria ascidiae* (Lank.) (par. *Ciona intestinalis*) in the intestinal epithelium. *a*, young stages showing the hypertrophy of the epithelial cells induced by the parasites at an early stage. *b*, older stage showing very great hypertrophy of the epithelial cell, with atrophy of its nucleus. *ep*, normal epithelial cell; *ep'*, hypertrophied epithelial cell containing (*G*) the young Gregarine; *n*, nucleus of normal cell; *n'*, nucleus of infected cell. (After Siedlecki, × 750.)

In many cases a Gregarine, after having been set free from an epithelial cell which it has destroyed, may secondarily attach itself again to the epithelium (Figg. 12 and 13). Although such secondary attachment may be exceedingly complicated, and may affect a large number of epithelial cells, as in *Pterocephalus* (Fig. 12), nevertheless it only produces mechanical alterations in the cells, and never has the marked effects which result from the primary attachment.

It is thus seen that the Gregarine destroys completely the cell in which it is parasitic at the commencement of its career. Nevertheless Gregarines appear to be extremely innocuous to their hosts. Since they do not reproduce themselves by schizogony, except in a very few instances, they do not overrun their host in the way that the Coccidia or Haemosporidia do. Though a given host often contains a considerable number of Gregarines, it must be supposed that they represent simply the batches of sporozoites derived from several distinct infections. The epithelial cell that each individual Gregarine has destroyed is not missed, and the injury is easily repaired. The nutriment that the Gregarines absorb in the gut of the host seems to be a tax lightly borne. There is, in short, no record of any pathological effects produced by these parasites beyond those already noted in the case of the host-cell.

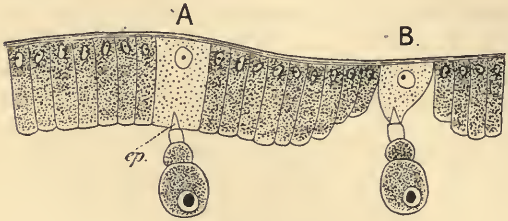

FIG. 11.

Effects produced on epithelial cells by the trophozoites of a Gregarine (*Pyxinia frenzeli*, Lav. et Mesn.) (par. *Attagenus pellio*, larva). *A*, hypertrophy of the cell (first stage). *B*, atrophy (second stage). Combined after figures by Laveran and Mesnil.

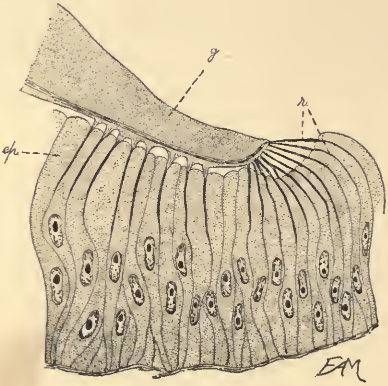

FIG. 12.

Portion of a section through the apparatus of fixation of a *Pterocephalus*, showing root-like processes extending from the Gregarine between the epithelial cells, which are not modified or altered in any way, but appear to be under the influence of traction exerted by the Gregarine. *g*, head of the Gregarine; *r*, root-like processes; *ep*, epithelial cells. (After Siedlecki, × 500.)

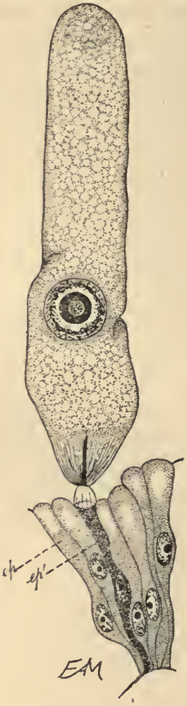

FIG. 13.

Trophozoite of *Lankesteria ascidiae* (Lank.) (par. *Ciona intestinalis*), attached by an anterior pseudopodium-like process to an epithelial cell (*ep'*), which is withered and apparently destroyed by it. *ep*, normal epithelial cells. (After Siedlecki, × 500.)

*Morphology and Life-history.*—Since a typical Gregarine has already been described in *Monocystis*, it is only necessary to review briefly the variations exhibited by this order as compared with the type selected for description.

The body-form and external characters of the trophozoite furnish sharp distinctions for classificatory purposes. The fundamental type of body-form may be described as a sphere or ovoid. In many species this type of form is very nearly retained (Fig. 22), especially in the non-motile coelomic forms, which often have a great resemblance to ova. More usually, however, the body becomes strongly elongated in one direction, a mode of growth correlated either with attachment by one pole or with forward movement in a definite direction. In many cases the body is extremely drawn out and attenuated, becoming vermiform in character (Fig. 1).

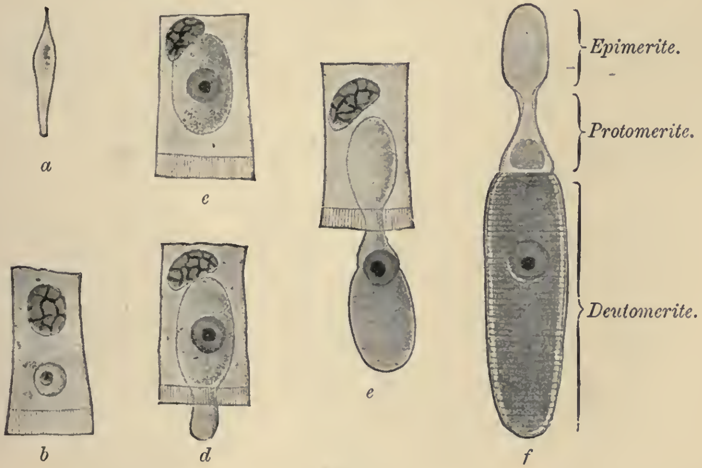

FIG. 14.

Scheme of development of a Gregarine from a sporozoite. *a*, free sporozoite ; *b* and *c*, stage in the growth of the parasite within an epithelial cell ; *d*, the Gregarine beginning to protrude from the cell ; *e*, segmentation of the body and emigration outwards of the nucleus, the intracellular portion of the body remaining as the epimerite ; *f*, adult Gregarine with three-chambered body. (From Wasielewski, after Schneider.)

In the sub-order Acephalina, of which *Monocystis* is an example, the body remains simple and is not subdivided into different regions, whatever its form. The Cephalina, however, are, with few exceptions, *septate*, that is to say, the body is divided by septa or partitions into distinct chambers or segments, usually three in number. The septate condition is brought about in the following way. The sporozoite penetrates an epithelial cell (Fig. 14, *b*) and grows within it into an oval body, which at an early stage cannot be distinguished in any way from a young Monocystid, or even from a Coccidian parasite (Fig. 14, *c*). Very soon, however, the young trophozoite grows out from the host-cell, and its nucleus travels out into that portion of the body which projects from the cell (Fig. 14, *d*, *e*). The free extremity of the Gregarine body continues to grow, while the intracellular portion becomes cuticularised and forms simply an organ of fixation, commonly called the *epimerite*. The extracellular Gregarine body becomes now divided by a septum into two chambers, one smaller proximal (*i.e.* nearer the host-cell and the epimerite), termed the *protomerite*, and one larger distal, termed the *deutomerite*, which usually contains the nucleus (Fig. 14, *f*); abnormal forms are sometimes found, however, in which the nucleus is lodged in the protomerite, owing apparently to precocious formation of the septum, before the nucleus had reached its distal position.

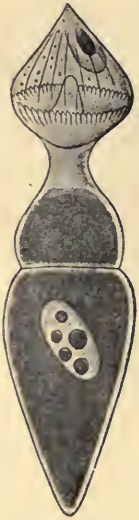

FIG. 15.

Cephalont of *Pyxinia rubecula*, Hamm. (par. *Dermestes* spp.) still attached by its epimerite to a detached epithelial cell. (From Wasielewski, after Léger.)

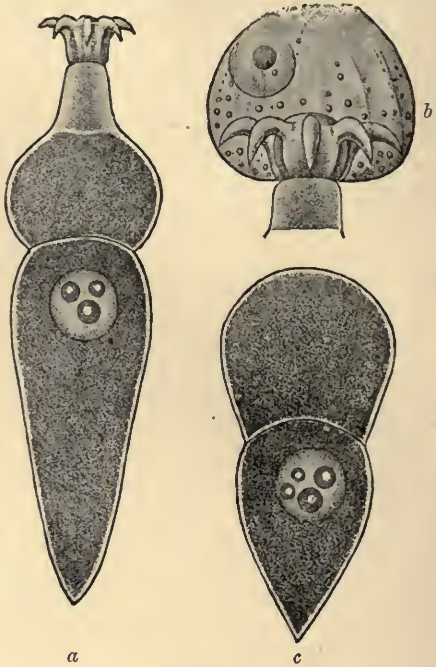

FIG. 16.

*Corycella armata*, Léger (par. *Gyrinus natator*, larva). *a*, cephalont; *b*, epimerite in the host-cell, magnified; *c*, sporont. (From Wasielewski, after Léger.)

The young trophozoite in the Cephalina remains attached to the host-cell for some time by its epimerite (Fig. 15). In this condition it is known as a *cephalont*. Soon it becomes detached and set free by a rupture of the junction between the epimerite and protomerite (Fig. 16). The epimerite remains sticking in the withered remains of the host-cell, and the Gregarine body, composed of protomerite and deutomerite, is free in the gut, where it continues its growth and further development. The free Gregarines are commonly termed *sporonts.*

The epimerites of Gregarines show every variety of size, shape, and pattern, and may be ornamented with hooks, spines, and other appendages (Fig. 17). They function as organs of attachment, as has been said, and probably also as organs of nutrition, since Laveran and Mesnil [16] have shown that they evoke changes in the host-cell which cannot be explained as the result simply of mechanical irritation. The possession of an epimerite is a feature which is used for classifying the Gregarines, and the legion Eugregarinae is separated into the two sub-orders Cephalina and Acephalina, according to the presence or absence of this appendage. As a general rule the forms which possess an epimerite have the body behind it divided into protomerite and deutomerite by a septum, and have hence been termed *Polycystida* seu *Septata* (Lank.), while those without an epimerite are also without a septum ; hence *Monocystida* seu *Haplocyta* (Lank.). But in one family, *Doliocystidae*, Labbé, an epimerite is present, and may attain a considerable size, as in *Doliocystis* (*Monocystis*) *aphroditae* (E. R. L.), without any septum dividing the rest of

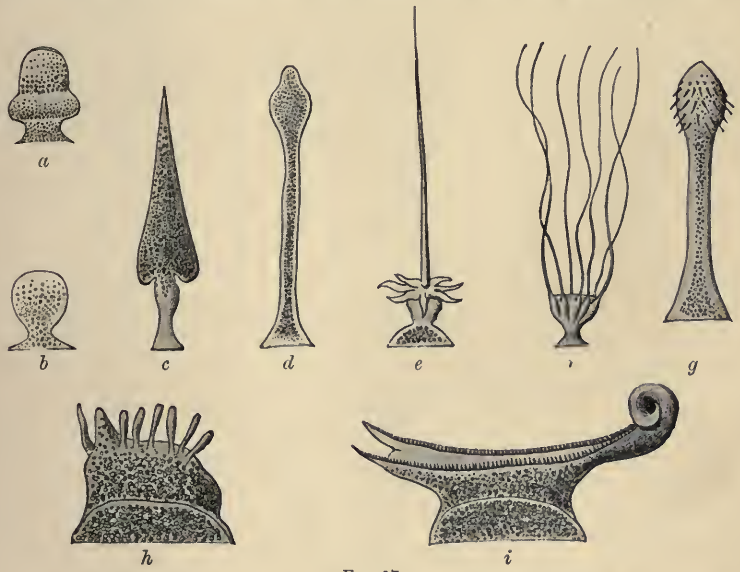

FIG. 17.

Epimerites of various Gregarines. *a*, *Gregarina longa* (Léger), (par. *Tipula* sp., larva) ; *b*, *Sycia inopinata*, Léger (par. *Audouinia* sp.) ; *c*, *Pileocephalus heerii* (Köll.), (par. *Phryganea*, larva) ; *d*, *Stylorhynchus longicollis*, Stein (par. *Blaps mortisaga*) ; *e*, *Beloides firmus* (Léger), (par. *Dermestes lardarius*, larva) ; *f*, *Cometoides crinitus* (Léger), (par. *Hydrobius* sp., larva) ; *g*, *Geneiorhynchus monnieri*, A. Schn. (par. *Libellula*, larva) ; *h*, *Echinomera hispida* (A. Schn.), (par. *Lithobius forficatus*) ; *i*, *Pterocephalus nobilis*, A. Schn. (par. *Scolopendra* spp.). (From Wasielewski, after Léger.)

the body (Fig. 19). It is purely a matter of definition whether these forms be considered as Cephalina without a septum, or as Monocystida with an epimerite. The Cephalina in which the body is non-septate are sometimes distinguished as Dicystida from those in which there is a distinct protomerite and deutomerite (Tricystida). These terms are to be understood, however, in a purely descriptive sense, and cannot be used for classificatory purposes, as there is no doubt that many dicystid species are derived from tricystid forms secondarily, by obliteration of the protomerite (Fig. 18). On the other hand, such forms as the *Doliocystidae* (Fig. 19) and *Selenidium* (Fig. 46) appear to be truly and primitively dicystid, and are to be regarded as intermediate forms transitional from Acephalina to Cephalina.

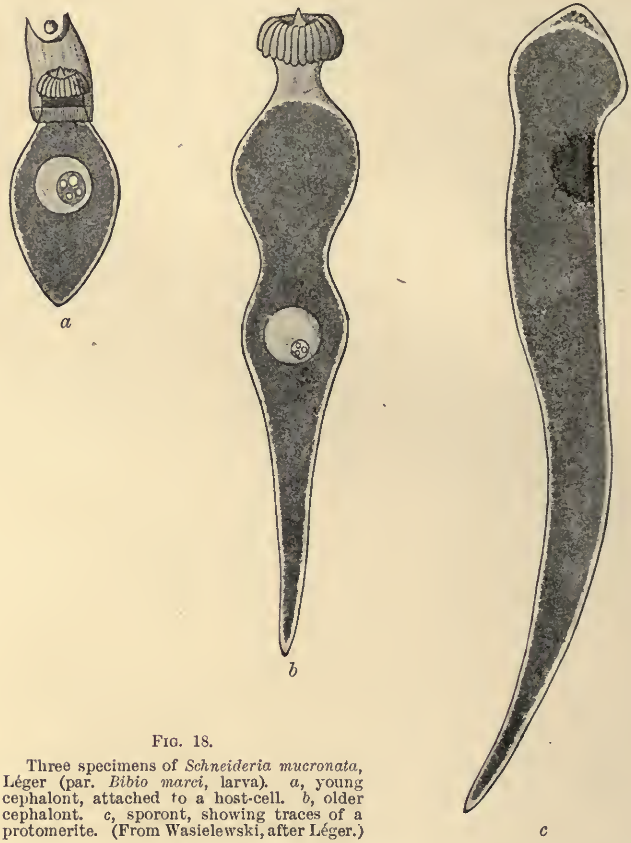

FIG. 18.

Three specimens of *Schneideria mucronata*, Léger (par. *Bibio marci*, larva). *a*, young cephalont, attached to a host-cell. *b*, older cephalont. *c*, sporont, showing traces of a protomerite. (From Wasielewski, after Léger.)

In the aberrant forms comprising the legion Schizogregarinae, the unsegmented body grows out into irregular processes, which give it an amoeboid appearance, whence these forms obtained their older name, Amoebosporidia. Recent observations have shown, however, that these processes are not pseudopodia, but are stiff outgrowths of the body, clothed by cuticle (Fig. 21), so that the name Amoebosporidia rests upon a misconception and must be abolished. The genus *Pterospora* is also remarkable for the possession of retractile processes, resembling tentacles (Fig. 37).

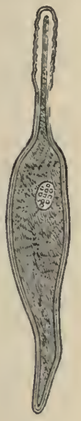

FIG. 19.

*Doliocystis aphroditae* (Lank.) (par. *Aphrodite aculeata*), a non-septate Gregarine with a distinct epimerite. (After Lankester.)

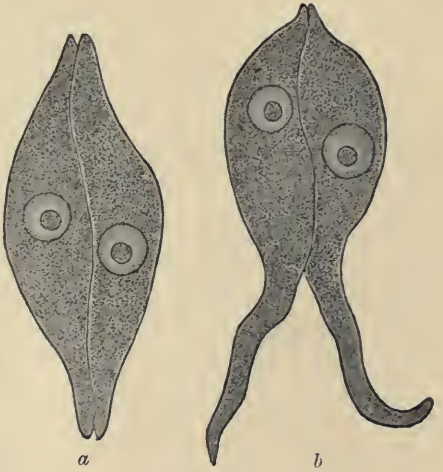

FIG. 20.

Associations of *Gonospora sparsa*, Léger, from the gut of *Glycera*. (From Wasielewski, after Léger.)

A curious feature of Gregarines, and one which has a marked influence in many cases on their external form and appearance, is their tendency to form associations during the trophic period, a peculiarity from which the type-genus *Gregarina* probably derives its name. In *Monocystis* it has been seen that two individuals come together when full-grown and become associated to form a cyst in common. In other Gregarines association may take place at a much earlier stage in the development of the individual (Fig. 20).

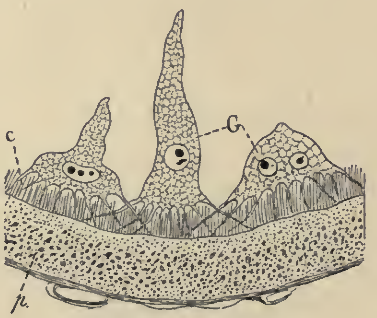

FIG. 21.

Portion of a section of a Malpighian tubule of *Blaps magica* infested by *Ophryocystis schneideri*, showing three individuals of the latter species (*G*), one of them with two nuclei, attached by stiff processes (the pseudopodia of Schneider) to the wall of the tubule. *p*, syncytial protoplasm of the tubule; *c*, cilia lining it. (After Léger and Hagenmüller, × 1500.)

In the *Diplocystis* found in the body-cavity of the cricket, young trophozoites become associated in couples almost immediately after leaving the host-cell, and, according to Cuénot, no solitary individuals are to be found above a certain size, since all the old maids die off. In *Diplocystis major* the two associates retain their distinctness, but in *Diplocystis minor* each couple becomes surrounded by a common membrane (Fig. 22). In *Cystobia holothuriae* early association has still more far-reaching results, since a fusion, complete except as regards the nuclei, of the two trophozoites takes place, so that the appearance of a single Gregarine with two nuclei is produced, with no trace of any septum between them (Fig. 23). While in the cases mentioned the association is undoubtedly a preliminary to the conjugation of gametes, it is more difficult to interpret the peculiar aggregations known as *syzygies* commonly seen in many species, especially amongst Cephalina. Free Gregarine individuals become attached to one another, the anterior extremity of one adhering to the posterior end of the other (Fig. 24, *a*). Usually such a syzygy consists of two individuals, but may be composed of a chain of half-a-dozen or more (Fig. 24, *c*). The most anterior individual is termed the *primite*, those behind it the *satellites*. The latter are always individuals which have lost their epimerites, if they belong to the Cephalina. The syzygy does not necessarily take the form of a simple chain. Two satellites may be attached side by side to the hinder end of the individual, primite or satellite, in front of them (Fig. 24, *b*). In some cases the individuals composing a syzygy are loosely attached and easily separated from one another, and the members of it are not modified in any way. In other cases the association is more intimate, and the satellite

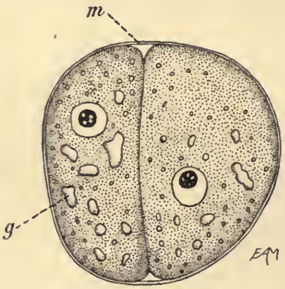

Fig. 22.

Precocious association in *Diplocystis minor*, Cuén., of the cricket. *m*, common membrane uniting the two associates; *g*, grains of albuminoid reserve material. (After Cuénot, × about 120.)

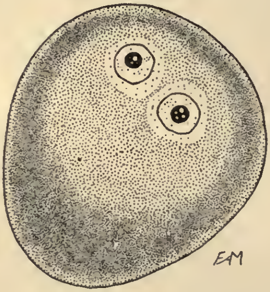

Fig. 23.

Adult trophozoite of *Cystobia holothuriae* (Ant. Schn.) (par. *Holothuria tubulosa*), showing the two nuclei, derived from the fusion of two individuals, but not separated by any septum. (After Minchin.)

or satellites may become modified in structure. In segmented forms this alteration affects chiefly the protomerite, which may be reduced or even absent. Thus in the genus *Didymophyes* syzygies of two individuals are formed in which the satellite loses its protomerite entirely, so that the resulting combination looks like a three-chambered Gregarine with two nuclei (Fig. 25, *a*).

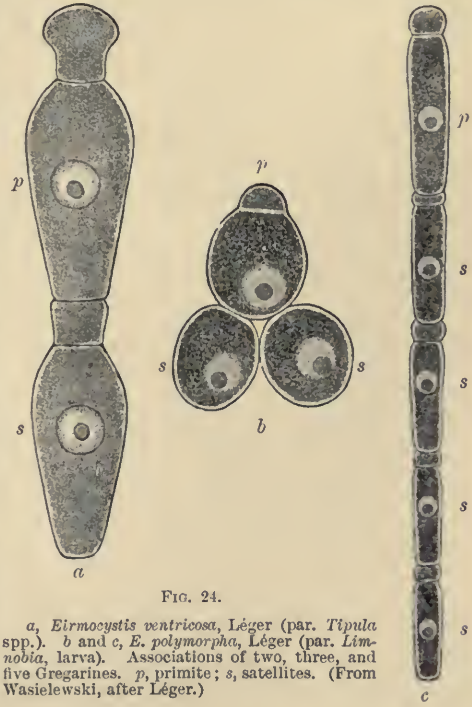

FIG. 24.

*a*, *Eirmocystis ventricosa*, Léger (par. *Tipula* spp.). *b* and *c*, *E. polymorpha*, Léger (par. *Limnobia*, larva). Associations of two, three, and five Gregarines. *p*, primite; *s*, satellites. (From Wasielewski, after Léger.)

Although in many cases the syzygies appear to be temporary attachments which have no connection with the subsequent reproductive phenomena, it is probable that as a general rule they represent associations of individuals destined to form conjugating gametes as described for *Monocystis*, especially in those cases where the union of primite and satellites is an intimate one, as in *Didymophyes* and others. Having regard to the manner in which conjugation takes place, there is no reason why any number of sporonts or gametocytes should not come together to form gametes within a common cyst, and the presence in a cyst of more than two sporonts appears to be of frequent occurrence in some species.

The body of a Gregarine trophozoite always consists of cuticle, ectoplasm, and endoplasm containing a nucleus, but each of these parts are subject to considerable variation in structure.

The cuticle or *epicyte* is a membrane secreted by the ectoplasm, usually of some thickness, and appearing doubly contoured in optical section (Fig. 26, *c*). Sometimes it can be broken up into fine vertical lamellae corresponding to the ridges presently to be described on the external surface. As has been said above, the cuticle is often produced into hooks or spines or other organs of fixation, especially on the epimerite. On the other hand, all such processes may be wanting entirely. The surface of the cuticle is not smooth, however, but has a delicately ribbed or fluted structure, producing fine striations which run in a meridional direction from pole to pole. As a rule there are no openings or visible pores of any kind in the cuticle, but, according to Siedlecki, a pore exists at the anterior end of *Lankesteria ascidiae*, from which is protruded a minute pseudopodium-like process which serves for the secondary attachment of the trophozoite to an intestinal cell of the host, and pores are stated to exist in the longitudinal furrows of the cuticle, as described below.

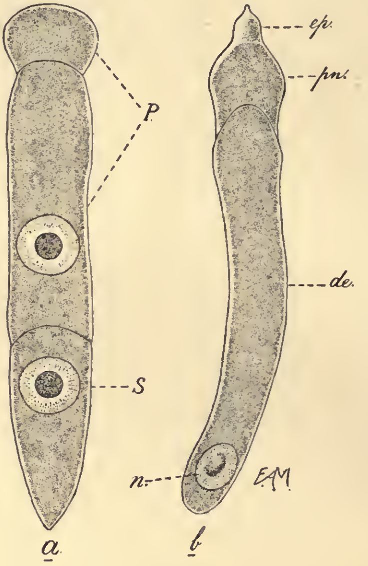

Fig. 25.

Trophozoites of *Didymophyes*. *a*, *D. paradoxa*, Stein (par. *Geotrupes stercorarius*), two associated sporonts; in the satellite the protomerite has disappeared. *b*, *D. gigantea*, Stein (par. *Oryctes nasicornis*), cephalont. *P*, primite; *S*, satellite; *ep*, epimerite; *pn*, protomerite; *dc*, deutomerite; *n*, nucleus.

The ectoplasm is a clear, hyaline layer of tougher protoplasm which in the motionless forms shows no special differentiation. But in most Gregarines, correlated with the power of active movement, the deeper layer of the ectoplasm contains a system of contractile fibrils, marking off a deeper *myocyte* from a more superficial *sarcocyte* layer of the ectoplasm (Fig. 26, *m.f*, *sc*). The sarcocyte is prolonged inwards to form the septum separating protomerite and deutomerite, when this division is found. The fibrils of the myocyte (Figg. 26, *m.f*, and 27) run in a more or less circular direction, with numerous oblique junctions and anastomoses, so that the system as a whole is more or less net-like.

The movements of Gregarines are often very active, though some forms appear perfectly motionless. Two kinds of movements are commonly seen. In the first place, the body manifests contractions of various kinds, without changing its place as a whole. It may bend and straighten again, or may exhibit ring-like constrictions which pass down the body in a manner resembling peristaltic movement. The latter is a very characteristic form of activity, and resembles greatly the "metabolic" form-changes seen in many Flagellata, such as *Euglena*, for which reason these movements were termed by Lankester "euglenoid." In the second place, many Gregarines possess the power of gliding forward at a great pace without any noticeable change of form, and without any apparent mechanism for producing their rapid progression.

The contractions and euglenoid movements of the Gregarine body are sufficiently accounted for by the myocyte-fibrillae, if the latter be assumed to be endowed with a power of contractility similar in its action to that of ordinary muscle-fibrils. But the gliding movements of Gregarines have always been a great puzzle.

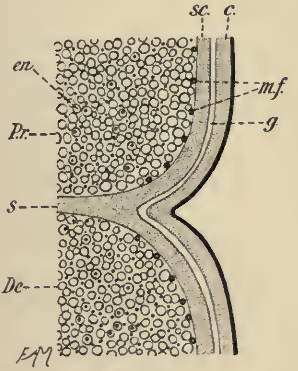

Fig. 26.

Longitudinal section of a Gregarine in the region of the septum between protomerite and deutomerite, semi-diagrammatic. *Pr*, protomerite; *De*, deutomerite; *s*, septum; *en*, endoplasm; *sc*, sarcocyte; *c*, cuticle; *m.f*, fibrils of the myocyte; *g*, gelatinous layer between sarcocyte and cuticle. (After Schewiakoff, × 2000 diameters.)

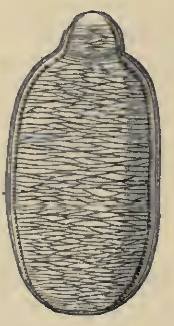

Fig. 27.

*Gregarina munieri* (A. Schn.), (par. *Timarcha tenebricosa*), showing the network of myocyte fibrillae. (From Lankester.)

The first satisfactory attempt at an explanation was given by Schewiakoff [26], who accounted for the forward progression by the extrusion of gelatinous fibres from the hinder end of the body. The fibres in question are derived from a clear homogeneous layer lying between the cuticle and the sarcocyte, and pass out from the body through minute slit-like pores in the furrows between the ridges of the cuticle; they then run backwards in the furrow towards the posterior end of the body, becoming stiffened by the action of the surrounding medium, and project free from the hinder end of the animal. The numerous threads thus produced form a hollow cylinder which by its continued growth and elongation pushes the Gregarine forward. Schewiakoff's explanation has met with general acceptance, but very recently it has been criticised by Crawley [12]. This author confirms the extrusion of a gelatinous substance, but denies that it is the cause or agency of progression, or could possibly be so in many cases, especially in the elongated serpent-like forms, such as *Porospora* *gigantea*, for example (Fig. 1). He attributes the forward progression to *transverse movements* of the body-surface, produced by the myocyte layer, and manifesting themselves "as a shifting of the cuticular striations in a direction at right angles to the long axis of the animal." A muscular impulse of this kind, starting anteriorly, passes along the body towards the hinder end, and causes differences in the contact of the body with surrounding objects. The wave of disturbance travelling along the surface of the body brings about a movement of the Gregarine in a direction opposite to that in which the impulse travels, and tends also to cause a swinging movement of the body from side to side, which, according to Crawley, can be observed very frequently in the forward progression, especially when the Gregarine encounters an obstacle in its path. Crawley thus refers the forward movement to the contractility of the myocyte, and points out that "in general, throughout the Sporozoa, the possession of muscle-fibres and the power of moving from place to place go hand in hand, while the forms which are not known to move lack muscular elements."

The endoplasm, the nutritive layer of the body, is of a more fluid nature than the ectoplasm, but does not exhibit any of the flowing movements often seen in other Protozoa. It is always crammed with great numbers of granular enclosures, representing reserve nutriment stored up for the reproductive period of the life-history. It is rare for the endoplasm to be vacuolated. The granules increase in number as the animal grows, and render the adult trophozoites very opaque, especially when they attain to a large size. The most abundant and largest kind of granules are the paraglycogen spherules, always present and sometimes attaining a diameter of 10 $\mu$. They consist of a substance allied to starch and glycogen, and are characterised by the following reactions: Iodine tinges them brown, changing into violet on addition of dilute sulphuric acid; they are not dissolved by pure acetic acid, weak mineral acids, alcohol, or ether; but they are soluble in dilute solution of potassium carbonate and in concentrated mineral acids. Other sorts of granules may be found in various Gregarines, but do not occur universally in all species. Such are the so-called carminophilous granules, of irregular form, and composed apparently of an albuminoid substance which is stained red by picrocarmine and acetocarmine, yellow by iodine; "pyxinin" granules, characteristic of the genus *Pyxinia;* fat-globules; and occasionally protein crystals and other more or less enigmatic enclosures.

The nucleus is always single, with the apparent exceptions due to precocious association already mentioned (Fig. 23). It has the form of a large spherical vesicle surrounded by a very distinct membrane, and appears in life as a clear space in the opaque, granular endoplasm. Within the membrane is a fluid nuclear sap in which float one or more karyosomes, held in place by a delicate nuclear reticulum. Each karyosome is usually a spherical body of vacuolated structure, as described for *Monocystis*. Sometimes the karyosome is drawn out and band-like (Fig. 44) or beaded. As a general rule, however, the nuclei of Gregarines exhibit a monotonous uniformity of structure and appearance.

The reproductive phase of the life-history is usually initiated, as has been said, by the association of two or more sporonts, but not infrequently a single Gregarine may become encysted by itself, without pairing with another. In this case the sporont breaks up into sporoblasts at once, a fact which may be expressed in another way by saying that the gametes develop without conjugation into spores, a proceeding which may be compared to parthenogenesis. In such cases the spores are smaller than those produced from zygotes.

The cyst is a structureless membrane secreted by the associated sporonts. Its function is to afford protection to the reproductive phases, and when once it is fully formed, subsequent development can proceed outside the body of the host. The cyst-wall consists commonly of a gelatinous outer layer, often of considerable thickness and showing concentric striations termed the *epicyst*, and a tough inner membrane, the *endocyst*. Some interesting mechanisms are found which have as their object the facilitation of the escape of the spores from the cyst. In the majority of cases the cysts dehisce by rupture of their walls, brought about by swelling of their contents, and in particular of the residual protoplasm, or by contraction and shrinkage of the cyst-wall, or by both causes combined. In other cases the residual protoplasm, after the sporoblasts are separated off from it, undergoes further development to produce a special mechanism. In the families *Dactylophoridae* and *Stylorhynchidae*, the residual protoplasm forms a compact mass which becomes surrounded by a membrane and gives rise to a structure termed a *pseudocyst*, which gradually swells until the true cyst-wall is burst asunder. In several genera of *Gregarinidae* ( = *Clepsydrinidae* auct.) the cysts are remarkable for the possession of *sporoducts* (Figg. 28 and 42), long tubular outgrowths through which the spores can pass out to the exterior. These ducts are also formed from the residual protoplasm, which take up a peripheral situation within the cyst, surrounding the more centrally placed spores. It then secretes a membrane immediately internal to the cyst-wall, and also gives rise to a variable number of tubes, usually six or eight, but sometimes only one, which at their first formation run inwards from the periphery of the cyst, but later become everted to form the sporoduct.

The conjugation, so far as it has been observed, conforms to the type described above for *Monocystis*, or takes place in a manner easily deducible from it (Fig. 29). In *Monocystis*, *Lankesteria*, *Diplocystis*, etc., there is perfect isogamy; the conjugating gametes are not distinguishable from one another, and do not fall into two classes. In the Cephalina, on the other hand, anisogamy of a highly differentiated type appears to prevail. In *Stylorhynchus* Léger [23] has recently described anisogamous conjugation of a very interesting type. Two sporonts associate and become encysted together: one of them gives rise to motile active gametes termed male, the other to non-motile passive gametes termed female. The sporonts themselves, therefore, may be considered to be potentially male and female. Each sporont occupies one-half of the cyst, so that a male and a female chamber can be distinguished. Each sporont breaks up into a number of primary sporoblasts or gametes, and at first the gametes formed in each chamber are simply little protoplasmic spheres (Fig. 30, *a*), as in

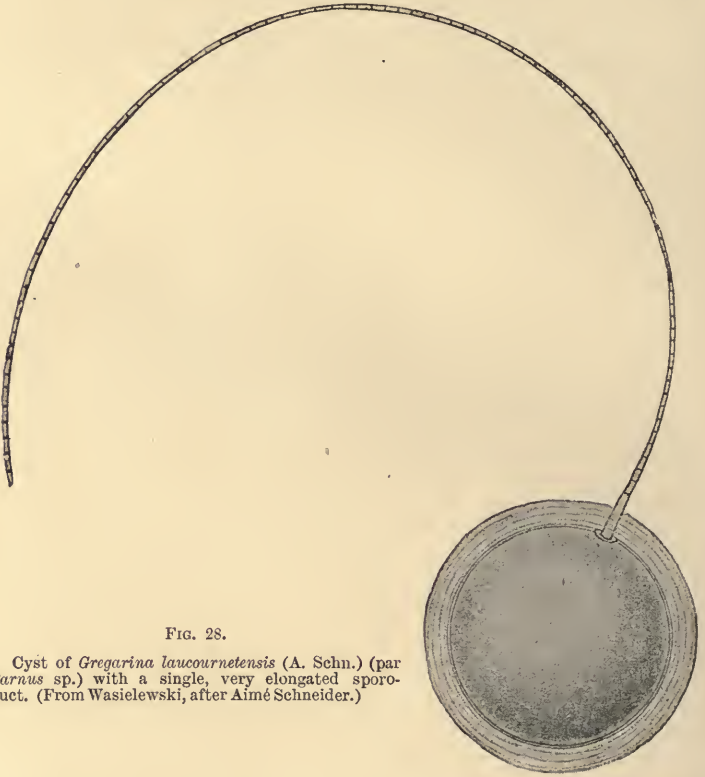

FIG. 28.

Cyst of *Gregarina laucournetensis* (A. Schn.) (par *Parnus* sp.) with a single, very elongated sporoduct. (From Wasielewski, after Aimé Schneider.)

*Monocystis*, but soon become differentiated. Those in the female chamber are smaller (about 7·5 $\mu$ in diameter), without much reserve material, and do not acquire any further structural peculiarities (Fig. 30, *e*). Those in the male chamber are larger and have more reserve material, and develop into motile gametes with the following structure (Fig. 30, *b*, *c*, *d*). The body is fusiform or cylindrical, about 13 $\mu$ in length, with an anterior clear and a posterior granular extremity. The anterior end is prolonged into a rostrum terminating in two little horn-like processes. The posterior end bears a flagellum about 27 $\mu$ in length. The nucleus is at the anterior pole of the body and consists of chromosomes not enveloped in any membrane. The flagellum is continued from the base forward through the body of the gamete as a delicate

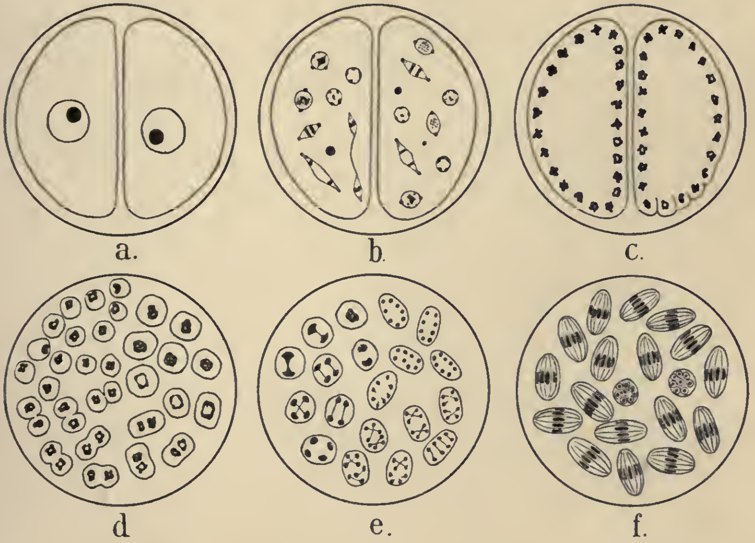

FIG. 29.

Schematic figures of conjugation and spore-formation in Gregarines, after Calkins, modified; the details of nuclear structure and division copied from Siedlecki's figures of *Lankesteria ascidiae* (E. R. L.). *a*, union of two sporonts in a common cyst. *b*, division of the nucleus of each sporont, showing various stages of division by mitosis, with very distinct centrosomes and without loss of the nuclear membrane. Fragments of the karyosomes are also seen, one on the left, two on the right. *c*, commencing formation of gametes. The very numerous minute, irregularly-shaped nuclei place themselves at the surface, and become segmented off, as seen on the lower side of the sporont on the right. (In *Lankesteria ascidiae* at this stage the sporonts become very irregular in shape and drawn out in various directions.) *d*, Stages in the conjugation of the gametes. In the left upper quadrant of the figure are seen separate gametes; in the left lower quadrant the gametes are seen uniting in pairs; the right lower quadrant shows the fusion of the nuclei; and in the right upper quadrant are seen complete zygotes or definitive sporoblasts. *e*, Stages in the division of the nuclei of the sporoblasts, which at the same time assume an oval form. The division of the nucleus takes place by the direct method into two, four, and eight small nuclei. *f*, cyst with ripe spores, each of which contains eight sporozoites derived from the eight nuclei of the sporoblast. Two spores are seen in cross-section.

axial filament which terminates in a deeply staining granule placed just behind the nucleus. The male gametes become free within the cyst and penetrate the female chamber, the rostrum being directed in front. They each seek out a passive female gamete and unite with it, often when still incompletely developed

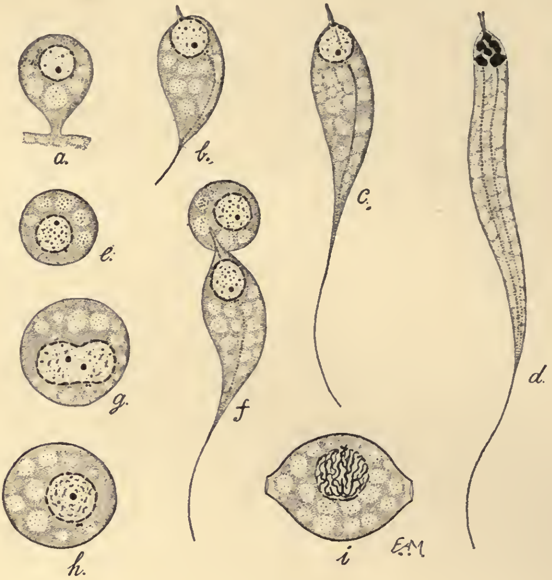

FIG. 30.

Development of the gametes, and fertilisation, in *Stylorhynchus longicollis*, Stein (par. *Blaps mortisaga*). *a*, undifferentiated gamete, still attached to the body of the parent gametocyte. *b*, *c*, *d*, stages in the evolution of the motile male gamete; the body elongates and becomes prolonged posteriorly into a vibratile caudal filament, the nucleus being placed at the anterior end, from which a short rostrum grows out; from the distinct centrosome an axial filament is prolonged through the body as far as the caudal filament, which appears to be a continuation of the axial filament; a prolongation of the axial filament in the opposite direction runs round the nucleus and forms the axis of the rostrum (Léger). The fully mature gamete, *d* ("spermatozoid," Léger), has the nucleus very condensed and the axial thread doubled, both in the body and in the rostrum; but as a rule the conjugation is hastened and takes place when the male gamete is in the still immature stage shown in *c* ("spermatid" of Léger). *e*, mature female gamete, only differing from *a* in the loss of the stalk attaching it to the parent body. *f*, a "spermatid" conjugating with a female gamete. *g*, later stage of the conjugation; the protoplasm of the two gametes has fused into a spherical mass and the nuclei are fusing. *h*, zygote (sporoblast), with single nucleus. *i*, spore, with spore-membrane and single nucleus preparing for division. (After Léger, × 1900.)

(Fig. 30, *f*). The flagellum drops off, but the bodies and nuclei of the gametes fuse and the zygote forms a spore in the usual way (Fig. 30, *g*, *h*, *i*). The conjugation occurring here is remarkable in that the gametes are the opposite, in some points of their equipment, to the general type of differentiation in anisogamy, since the active male element is as large or larger than the passive female, and as well provided with reserve material. In *Pterocephalus*, on the other hand, Léger and Duboscq [24] have described conjugation between gametes differentiated in a manner more in accordance with accustomed types of anisogamy. The gametes formed in the female chamber resemble telolecithal ova, having the nucleus situated in a patch of formative protoplasm at one pole, while the rest of the cell is occupied by coarse vitelline granules. The male gametes, on the contrary, are very minute, like those of Coccidia, and consist almost entirely of chromatin substance, nearly the whole protoplasmic body of the male gametocyte being left behind in the male chamber as residual protoplasm, from which the pseudocyst (see above, p. 183) is formed. The body of each microgamete is described as being filamentous, 5 or 6 $\mu$ in length, with a refringent rostrum anteriorly and a flagellum,

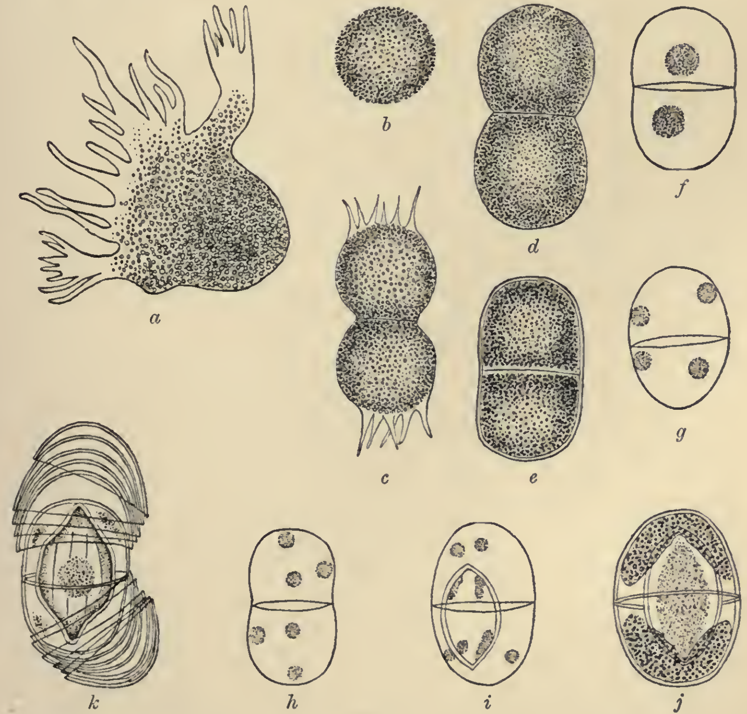

FIG. 31.

Stages in the life-history of *Ophryocystis bütschlii*, A. Schn (par. *Blaps mortisaga*). *a*, large multinucleate trophozoite with pseudopodium-like processes. *b*, small trophozoite with one nucleus, produced by the dividing up of a large individual. *c*, *d*, *e*, association and encystment of two sporonts. *f*-*h*, division and diminution of nuclei. *i*, single spore formed from the zygote, with two residual nuclei in each half of the cyst. *j*, cyst with single spore and two masses of residual protoplasm. *k*, ripe cyst with epicyst formed in numerous separate layers and endocyst enclosing the single spore and the remnants of the residual protoplasm. (From Wasielewski, after A. Schneider.)

about double the length of the body, posteriorly, and as bearing an undulating membrane which runs in a loose spiral from the rostrum to the base of the flagellum. The microgametes fertilise the "ova" in the usual way.

Another and interesting variation in the type of conjugation has been described by Léger [21] in the genus *Ophryocystis* of the Schizogregarinae. Here perfect isogamy obtains, combined with reduction of the gametes. The sporonts become encysted together, separated at first by a septum (Fig. 31, *c-f*). In each the nucleus divides into two, and one daughter nucleus degenerates (Fig. 31, *g*). The remaining nucleus divides again, and again one daughter nucleus degenerates (Fig. 31, *h*). The survivor is the pronucleus and represents one-fourth of the nucleus of the sporont. The protoplasm of the sporont condenses round it to form a single gamete, leaving a large quantity of residual protoplasm containing the degenerating nuclei. The two gametes derived in this way, each from one of the original sporonts, fuse, the septum becoming absorbed. Thus in each cyst is formed a single zygote (Fig. 31, *i, j*), which develops into the single spore, containing when ripe the usual eight sporozoites. Sometimes, however, the septum is not absorbed, and each gamete then develops parthenogenetically, so that the cyst contains two small spores instead of a single large one. It is evident that this condition is to be derived from that in *Monocystis* by reduction and degeneration of all the gametes formed from each gametocyte except one. In the allied genus *Schizocystis* numerous gametes are formed from each sporont, and conjugate after the manner of *Monocystis*.

The spores of Gregarines are either naked gymnospores or chlamydospores, invested by a tough envelope. The former condition is uncommon, but is found in two genera of Cephalina. In the first of these, the genus *Aggregata*, Frenzel, the gymnospores or sporozoites are scattered in the cyst round several residual masses of protoplasm, giving a certain resemblance to the cysts of the malarial parasites formed in the stomach of the mosquito (Fig. 32). In the second, the genus *Porospora*, A. Schn., sporoblasts are formed, each of which gives rise to very numerous sporozoites grouped round a central mass of protoplasm,

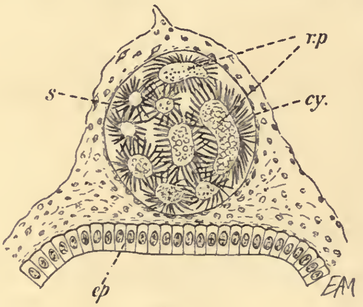

Fig. 32.

Portion of a section of the intestine of *Pinnotheres* passing through a coelomic cyst of *Aggregata coelomica*, Léger. The numerous sporozoites (*s*) are arranged radially round masses of residual protoplasm (*r.p*). *cy*, cyst-wall; *ep*, intestinal epithelium. (After Léger, × 180.)

and each such cluster of sporozoites resembles to a certain extent an ordinary Gregarine spore, but has no enveloping membrane or sporocyst (Fig. 41). *Aggregata* and *Porospora* are grouped together as a tribe Gymnosporea in distinction to the ordinary Gregarines, the Angiosporea, in which a chlamydospore is formed. The protoplasm of the sporonts may, in some cases, be entirely used up to form sporoblasts, in which the sporulation is said to be *complete*, but more often it is *incomplete*, with a more or less considerable mass of residual protoplasm.

The typical Gregarine spore contains eight sporozoites, and is therefore said to be *octozoic*, but exceptionally only four sporozoites are formed, as in *Selenidium*, hence *tetrazoic*. The sporozoites are grouped in very various ways round a granular mass of residual protoplasm, which contains the last remnants of the reserve nutrition stored up by the sporont. The protoplasm of the sporozoites is clear and finely granulated. Each sporozoite is typically sickle-shaped with the nucleus in the middle. Sometimes the nucleus is at one extremity, and the sporozoite then has a form more resembling a tadpole (Fig. 38).

The spore-envelope or sporocyst consists of two layers, an outer clear and delicate *epispore*, and an inner refringent and tough *endospore*. Sometimes these two layers are quite separate, or, on the other hand, they may be intimately united. In external characters the spores show the greatest possible variety of form and pattern, and are frequently ornamented with long tails or processes, which may vary considerably even in closely allied species, as in the species of *Cystobia* infesting Holothurians (Fig. 38). Another remarkable feature seen in some genera is the union of the spores by their sporocysts to form strings or ropes ("spores en chapelet") (Fig. 34, *f*).

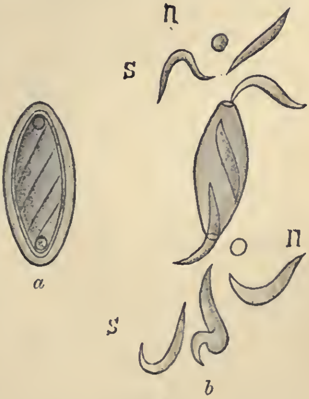

Fig. 33.

Spores of *Pyxinia rubecula*, Hamm. (par. *Dermestes* spp.). *a*, a ripe spore showing distinct epispore and endospore. *b*, the endospore set free after bursting of the epispore. After extrusion of two *polar spheres* (*n*), the sporozoites (*s*) escape from the spore. (From Wasielewski, after Léger.)

With regard to the dissemination of the spores, and the manner in which they infect new hosts, there is nothing to add to what has been stated above with regard to *Monocystis* (p. 163) and Sporozoa generally (p. 166). In no case is a true intermediate host known to occur. The life-cycle of Gregarines is, in the vast majority of cases, monogenetic, and consists of sporogony only, as described above for *Monocystis*. The cases in which proliferation, by other methods than the usual spore-formation, has been alleged, are for the most part very doubtful, and, though not incredible, are highly improbable for reasons already put forward in dealing with *Monocystis*. There are, however, a few well-attested cases of schizogony, which is correlated in Eugregarinae, as shown by Caullery and Mesnil [10], with an intracellular stage of long duration, and takes place during this phase of the life-history. Thus in *Gonospora longissima*, Caull. et Mesn., from the Annelid *Dodecaceria concharum*, the nucleus of the intracellular trophozoite multiplies by division, and the body divides into six or eight merozoites arranged as a "corps en barillet" (see p. 222). The merozoites then separate, escape from the host-cell, and develop into the intercellular sporonts. Another and similar case has been

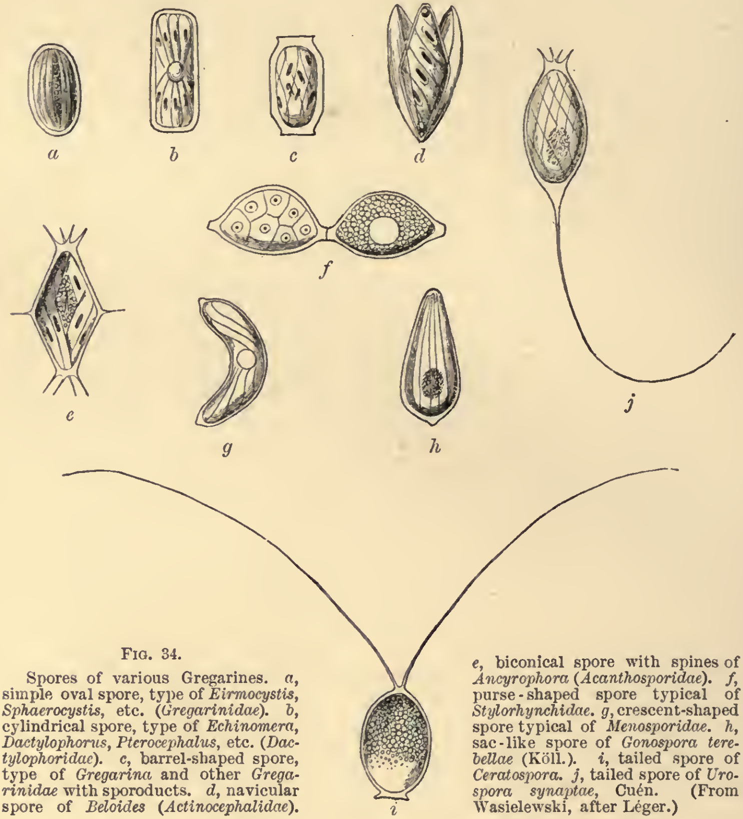

FIG. 34.

Spores of various Gregarines. *a*, simple oval spore, type of *Eirmocystis*, *Sphaerocystis*, etc. (*Gregarinidae*). *b*, cylindrical spore, type of *Echinomera*, *Dactylophorus*, *Pterocephalus*, etc. (*Dactylophoridae*). *c*, barrel-shaped spore, type of *Gregarina* and other *Gregarinidae* with sporoducts. *d*, navicular spore of *Beloides* (*Actinocephalidae*). *e*, biconical spore with spines of *Ancyrophora* (*Acanthosporidae*). *f*, purse-shaped spore typical of *Stylorhynchidae*. *g*, crescent-shaped spore typical of *Menosporidae*. *h*, sac-like spore of *Gonospora terebellae* (Köll.). *i*, tailed spore of *Ceratospora*. *j*, tailed spore of *Urospora synaptae*, Cuén. (From Wasielewski, after Léger.)

observed by Caullery and Mesnil [8*b*][1] in a species of *Selenidium* from *Spio fuliginosa.* In the Schizogregarinae, on the other hand, schizogony is of constant occurrence, as their name implies, and takes the form of multiple fission during the free extracellular phases of the life-history.

## CLASSIFICATION.

The systematic arrangement of the Gregarinida that follows is taken from Labbé's "Sporozoa" [4], for the most part, but with some additions or modifications necessitated by recent advances in our knowledge of the group.

SUB-ORDER I. SCHIZOGREGARINAE, Léger (*Amoebosporidia* auct.). Gregarinida in which schizogonic reproduction takes place during the extracellular phase of the trophozoite, in addition to the ordinary sporogony.

The forms composing this sub-order have been regarded until recently as a very problematic group. Their position in the Sporozoa and their affinities with other members of the class have been considered doubtful and altogether uncertain. Up to the end of the nineteenth century the group was represented only by two species of *Ophryocystis*, except for the fact that the supposed cancer-parasite has been referred to it by some authorities. The misconception which has prevailed with regard to the natural position of these forms appears to be largely due to the fact that the species of *Ophryocystis* were originally described as amoeboid, and this character was supposed to be diagnostic of the order represented by them, hence termed Amoebosporidia.

The recent investigations of Léger [20, 21, 25], however, have not only made known an allied form, *Schizocystis*, which has a fixed body-form like other Gregarines, but have demonstrated that even *Ophryocystis* is not amoeboid, as originally described, but has a definite orientation of the body, the apparent pseudopodia being merely stiff processes of attachment (Fig. 21). There can be no question that the natural position of the group is amongst the Gregarines ; indeed it is difficult to find any constant diagnostic character, except the mode of reproduction, separating *Ophryocystis* and *Schizocystis*, the only two genera known at present, from the rest of the order.

Genus 1. *Schizocystis*, Léger, 1900, for *S. gregarinoides*, Léger, from the intestine of a dipterous larva, *Ceratopogon* sp. The trophozoites are cylindrical and elongated, about 150 $\mu$ in length, with an anterior clearer region, and occur fixed to depressions in the intestinal wall. They resemble a Monocystid in general appearance, but while uninucleate in the youngest stages, the full-sized individuals may have as many as sixty nuclei. The body then divides up to form a number of merozoites, which become trophozoites of the second generation. The latter are uninucleate, and when full-sized they associate and become encysted, giving rise to gametes which conjugate and produce octozoic spores, exactly after the pattern of *Monocystis*. Genus 2. *Ophryocystis*, A. Schneider, 1884. Several species are known, all from the Malpighian tubules of beetles; type-species *O. bütschlii*, A. Schn., from *Blaps mortisaga* (Fig. 31). The body of the trophozoite is of irregular form, with pseudopodium-like processes (Figg. 21, 31, and 35). The trophozoites of the first generation have several nuclei (apparently not more than six or eight) when full-sized, and then divide up to form as many small individuals of the second generation, which often remain connected together for some time (Fig. 35, *a*, *d*), but ultimately separate and become the uninucleate trophozoites of the second generation. The latter, when adult, associate and become encysted, and then give rise to a single octozoic spore, after elimination of nuclei and conjugation of a surviving pair, as described above (p. 188).

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[1] Whose figures, however, are far from convincing.

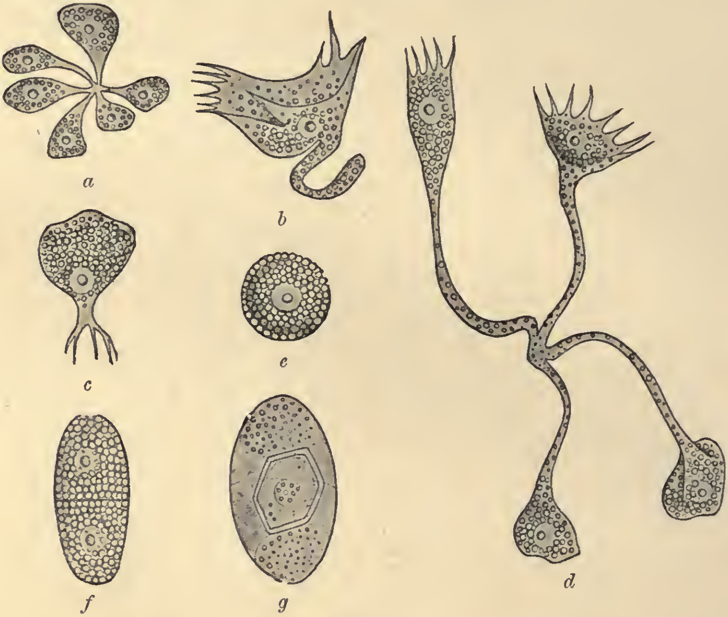

FIG. 35.

Stages in the life-history of *Ophryocystis francisci*, A. Schn. (par. *Akis* spp.). *a*, rosette of six small uninucleate individuals produced by division of a schizont; *b* and *c*, individuals detached from a rosette, in *b* still showing the process of attachment; *d*, rosette of four individuals; *e*, sporont; *f*, association of two sporonts; *g*, cyst with single spore and two masses of residual protoplasm. (From Wasielewski, after A. Schneider.)

SUB-ORDER II. EUGREGARINAE, Léger. Gregarinida in which schizogonic reproduction is of very exceptional occurrence, and takes place only during the intracellular phase, if at all. Spores octozoic with the rarest exceptions.

TRIBE 1. ACEPHALINA, Kölliker (*Monocystidea*, Stein). Eugregarinae in which the body is non-septate, and without an epimerite at any stage. Chiefly "coelomic" parasites.

Genus 3. *Monocystis*, Stein, 1848. Trophozoites characterised by considerable contractility, and consequent changeability of body-form. Spores navicular. Several species from Oligochaetes, one from *Clymenella torquata*, and one from *Diaptomus* and *Cyclops*, all inhabiting the vesiculae seminales or general body-cavities of their hosts. Type *M. agilis*, Stein (Figg. 2-8). The genus *Spermatophagus*, Labbé, 1899 (nom. nov. for *Spermatobium*, Eisen, 1895, preoccupied), for two species parasitic in the vesiculae seminales of earthworms, is apparently a synonym of *Monocystis*. Genus 4. *Zygocystis*, Stein, 1848. Adult trophozoites generally piriform, always found associated in couples or threes (Fig. 36); spores biconical. Type *Z. cometa*, Stein, from the vesiculae seminales and general body-cavity of *Lumbricus agricola*. Two other species are known. Genus 5. *Zygosoma*, Labbé, 1899 (nom. nov. for *Conorhynchus*, Greeff, 1880, preoccupied). Trophozoites pear-shaped, the entire body covered with finger-like processes, the endoplasm filled with vacuoles; always associated in couples when full-grown. Sporulation unknown. Unique species *Z. gibbosum* (Greeff) from the gut of *Echiurus pallasii*. Genus 6. *Pterospora*, Racovitza and Labbé, 1896. Trophozoites pear-shaped, the smaller extremity bearing two groups of finger-shaped retractile processes, four in each group; always found associated in couples. Spores with dissimilar poles, the epispore prolonged into three lateral wing-like expansions. Unique species *P.*

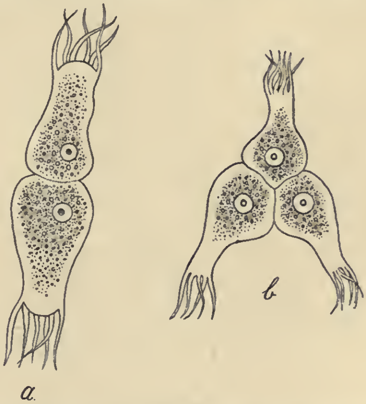

Fig. 36.

*Zygocystis cometa*, Stein (par. *Lumbricus communis* [=*herculeus*?]). *a*, syzygy of two individuals; *b*, of three. (After Stein, × 250.)

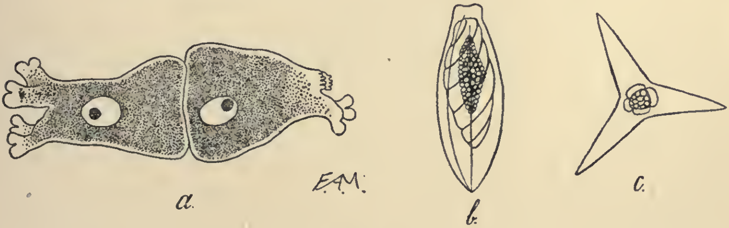

Fig. 37.

*Pterospora maldaneorum*, Rac. et Lab. (par. *Liocephalus liopygus* and *Clymene lumbricalis*). *a*, two associated trophozoites; the individual on the left is fully expanded, that on the right is commencing to retract its processes. *b*, spore showing the sporozoites coiled spirally round the central mass of granular residual protoplasm. *c*, transverse section of a spore showing the three wing-like processes and the sporozoites (four of them) in the section round the central residual protoplasm.

*maldaneorum*, R. and L. (Fig. 37), from the coelom of *Liocephalus liopygus* and *Clymene lumbricalis*. Genus 7. *Cystobia*, Mingazzini, 1891. Trophozoites large, oval or irregular in form, with two nuclei, resulting probably from early fusion of associated individuals (Fig. 23). Spores with dissimilar poles, the epispore forming a funnel-like projection at one pole, sometimes also a tail-like expansion at the other (Fig. 38). Parasites of Holothurians occurring in the blood-vessels, whence the cysts dehisce into the coelom. Type *C. holothuriae* (Ant. Schn.) from *Holothuria tubulosa*. Genus 8. *Lithocystis*, Giard, 1876. Trophozoites large, ovoid or vermiform, with the endoplasm filled with crystals of calcium oxalate. Spores with long tubular processes of the epispore at one pole. Unique species *L. schneideri*, Giard (Fig. 39), from the coelom of various Echinids. Genus 9. *Ceratospora*, Léger, 1892. Trophozoites of elongated conical form, associating by their truncated extremity, and giving rise to spores without encystment and without change of external form. Spores oval, with a collar-like expansion at one extremity, and two long rigid filaments at the other (Fig. 34, *i*). Unique species *C. mirabilis*, Lég., from the body-cavity of *Glycera* sp. Genus 10. *Urospora*, A. Schneider, 1875. Trophozoites large, spores oval, with a caudal filament at one pole (Fig. 34, *j*). *U. saenuridis* (Köll.), from the vesiculae seminales and coelom of *Tubifex rivulorum*. Other species from Nemertines, *Sipunculus*, *Synapta*, etc. Genus 11. *Gonospora*, A. Schneider, 1875. Trophozoites ovoid, piriform, or vermiform (Fig. 20). Spores with dissimilar poles, rounded at one extremity, bearing one or more tooth-like processes at the other (Fig. 34, *h*). Four species, all from the coelomic cavities of Polychaeta. Type *G. terebellae* (Köll.), from *Terebella*, etc. Genus 12. *Syncystis*, A. Schneider, 1886. Trophozoites ovoid or piriform. Spores navicular with four divergent bristles at each extremity. Unique species *S. mirabilis*, A. Schn., from the body-cavity and fat-body of *Nepa cinerea*. Genus 13. *Diplocystis*, Künstler, 1887. Trophozoites of "coelomic" habitat, associating precociously to form spherical masses. Spores spherical or oblong. *D. schneideri*, Künst., from the body-cavity of *Periplaneta americana*. *D. major*, Cuén., and *D. minor*, Cuén. (Fig. 22), from the common cricket. Genus 14. *Lankesteria*, Mingazzini, 1891. Trophozoites more or less spatulate (Fig. 13). Spores oval (compare Fig. 29, *f*). Type *L. ascidiae* (Lank.), from the gut of *Ciona intestinalis*. The sporozoan parasite described by Pollard,[1] from the intestinal epithelium of *Amphioxus*, is identified by Labbé as the intracellular stage of a Gregarine belonging to this genus. Genus 15. *Callyntrochlamys*, Frenzel, 1885. Trophozoites with the body constricted into two regions not separated by any septum, and with a fur-like covering of rods, resembling cilia, clothing the surface of the

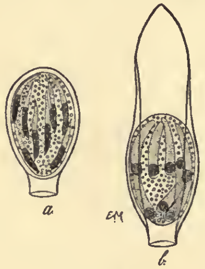

FIG. 38.

Spores of *a*, *Cystobia irregularis* (Minchin), (par. *Holothuria forskalii*); *b*, *C. holothuriae* (Ant. Schneider), (par. *Holothuria tubulosa*). (After Minchin.)

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[1] *Quart. Journ. Micr. Sci.*, N.S. xxxiv. p. 311.

body except at the anterior extremity. Spores not described. Type *C. phronimae*, Frenz., from the gut of *Phronima sedentaria.* Genus 16. *Ancora*, Labbé, 1899 (nom. nov. for *Anchorina*, Ming., 1891, preoccupied). Trophozoite anchor-shaped, with two anterior lateral prolongations of the body. Spores unknown. Unique species *A. sagittata* (Leuck.), from the gut of *Capitella capitata.*

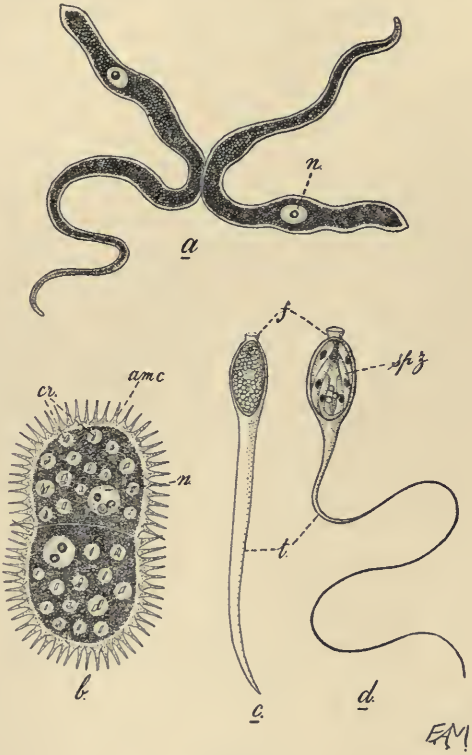

Fig. 39.

*Lithocystis schneideri*, Giard (par. *Echinocardium*, etc.). *a*, an association of two of the extremely lively trophozoites, which attach themselves loosely to one another in pairs, keeping up at the same time very active movements. *b*, two trophozoites (sporonts) about to become encysted; the bodies have contracted into compact motionless masses, and in each individual vacuoles have appeared containing clinorhombic crystals of calcium oxalate; the whole mass is surrounded by a coat of amoebocytes from the coelomic fluid of the host. *c*, an unripe spore, before formation of sporozoites, highly magnified. *d*, a ripe spore. *c* and *d* also show the differences between the two kinds of spores; *c* is a microspore, *d*, a macrospore. *n*, nucleus; *am.c*, investment of amoebocytes; *cr*, crystals; *f*, funnel-like prolongation of the epispore, through which the sporozoites pass out; *t*, tail-like process of the epispore, tubular in the unripe, filamentous in the ripe spore; *sp.z*, sporozoites. (After Léger.)

The following genera of Acephalina, known only in the trophozoite phase, are insufficiently characterised :—

Genus 17. *Pleurozyga*, Mingazzini, 1891. Trophozoites more or less claviform, associating laterally. Three species from Ascidians. Genus 18.

*Ophioidina*, Mingazzini, 1891. Trophozoites elongated, vermiform, the body cylindrical, blunt at one end, pointed at the other. *O. bonelliae*, Frenz., from the gut of *Bonellia viridis*. Two other species are also referred to this genus. Genus 19. *Köllikerella*, Labbé, 1899 (nom. nov. for *Köllikeria*, Ming., 1893, preoccupied). Trophozoites of rhomboidal form, the anterior extremity rounded and forming a sort of head, separated by a constriction from the rest of the body. Unique species *K. staurocephali* (Ming.), from *Staurocephalus rudolphii*. Genus 20. *Lobianchella*, Mingazzini, 1891. Trophozoites of elongated form with the anterior end rounded. Unique species *L. beloneides*, Ming., from the coelom of *Alciope* sp.

TRIBE 2. CEPHALINA, Delage (= *Polycystidea* auct. + *Doliocystidae*). Eugregarinae which always possess an epimerite, which may be present only in the young stages or may be a permanent organ. The body is divided, typically, by a septum into protomerite and deutomerite, but may be simple, non-septate. Parasites chiefly of Arthropods, usually occurring in the gut.

(*a*) SUB-TRIBE GYMNOSPOREA, Léger. The cyst contains naked gymnospores (sporozoites) not enveloped in sporocysts to form spores.

FAMILY 1. AGGREGATIDAE, Labbé. Sporonts septate, forming associations of two or more individuals. Sporozoites grouped irregularly round a number of residual masses (Fig. 32).

Genus 21. *Aggregata*, Frenzel, 1885. Trophozoites elongated, cylindrical. *A. portunidarum*, Frenz., from the intestine of *Carcinus maenas* and *Portunus arcuatus*, and several other species from other Crustacean hosts.

FAMILY 2. POROSPORIDAE, Labbé. Each sporoblast gives rise to numerous sporozoites grouped round a residual mass, but the "spores" so formed are not enveloped in sporocysts (Fig. 41).

Genus 22. *Porospora*, A. Schneider, 1875. Epimerite minute, button-like. Trophozoites large, septate, usually solitary (Fig. 1), sometimes associated (Fig. 40). Unique species *P. gigantea* (E. v. Ben.), from the gut of the lobster.

(*b*) SUB-TRIBE ANGIOSPOREA, Léger. Spores well developed, with double sporocysts composed of epispore and endospore.

FAMILY 3. GREGARINIDAE, Labbé (*Clepsydrinidae*, Léger). Trophozoites with simple epimerites (Fig. 17, *a*). Cysts with or without sporoducts. Spores oval, in forms without sporoducts (Fig. 34, *a*), but in forms with sporoducts they are barrel-shaped (Fig. 34, *c*) and united in strings by their flattened ends.

Genus 23. *Gregarina*, Dufour, 1828 (*Clepsydrina*, Hammerschmidt, 1838). Epimerite conical or knobbed, rarely large. Cysts spherical or oval with sporoducts (Figg. 28 and 42). Spores barrel-shaped (Fig. 34, *c*). *G. blattarum*, Sieb. (Fig. 42), from the common cockroach *Periplaneta orientalis*; *G. ovata*, Duf., from the earwig *Forficula auricularia*; *G. polymorpha* (Hamm.), from the meal-worm; and numerous other species, parasitic in the intestinal tracts of insects. Genus 24. *Gamocystis*, A. Schneider, 1875. Trophozoite with transitory protom., resembling a monocystid. Cyst with sporoducts. Spores elongated,

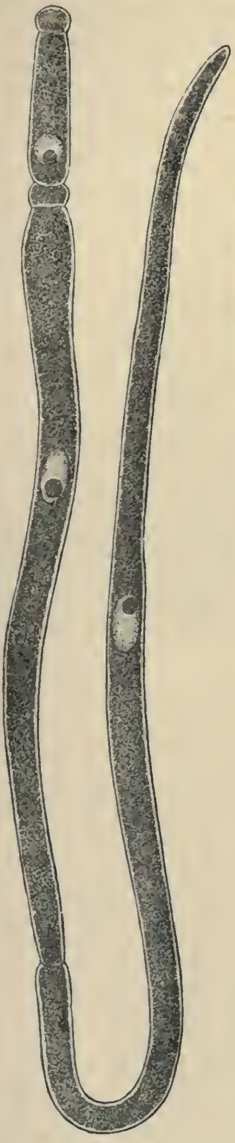

Fig. 40.

*Porospora gigantea*, v. Ben. Association of three individuals adhering to one another, of which the hindermost has no obvious protomerite. (From Wasielewski, after Léger.)

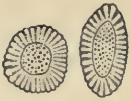

Fig. 41.

Two spores of *Porospora gigantea*, v. Ben. (par. *Homarus vulgaris*), showing the numerous sporozoites planted round a central mass of residual protoplasm. (From Lankester.)

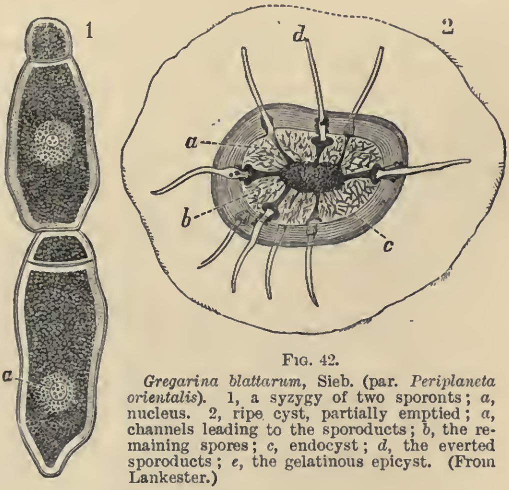

Fig. 42.

*Gregarina blattarum*, Sieb. (par. *Periplaneta orientalis*). 1, a syzygy of two sporonts; *a*, nucleus. 2, ripe cyst, partially emptied; *a*, channels leading to the sporoducts; *b*, the remaining spores; *c*, endocyst; *d*, the everted sporoducts; *e*, the gelatinous epicyst. (From Lankester.)

cylindrical. *G. tenax*, A. Schn., from the gut of the cockroach *Ectobia lapponica*; *G. ephemerae*, Frantz, from the intestine of *Ephemera*, larva. Genus 25. *Eirmocystis*, Léger, 1892 (*Hirmocystis*, Labbé, 1899). Epim. a conical knob. Sporonts forming syzygies of numerous individuals (Fig. 24). Cysts without sporoducts. Spores oval in form (Fig. 34, *a*). *E. polymorpha*, Léger, from the intestine of *Limnobia*, larva, and other species from the digestive tracts of insects. Genus 26. *Hyalospora*, A. Schneider, 1875. Cysts without sporoducts. Spores ellipsoidal, pointed at the ends, bulging in the middle. *H. roscoviana*, A. Schn., type-species, from the gut of *Petrobius maritimus*, and two other species. Genus 27. *Euspora*, A. Schneider, 1875. Cysts without sporoducts. Spores prismatic. Unique species *E. fallax*, A. Schn., from the gut of *Rhizotrogus aestivus*. Genus 28. *Sphaerocystis*, Léger, 1892. Body of trophozoite spheroidal, with transitory protom. Cysts without sporoducts. Spores oval in form (Fig. 34, *a*). Unique species *S. simplex*, Lég., from the gut of *Cyphon pallidus*, larva. Genus 29. *Cnemidospora*, A. Schneider, 1882.

Epim. large, lancet-shaped. Sporonts solitary, the body elongated and cylindrical in form, with globular protom. Cysts without sporoducts. Spores ellipsoidal with thick sporocysts. Unique species *C. lutea*, A. Schn., from digestive tract of *Glomeris* sp. Genus 30. *Stenophora*, Labbé, 1899 (nom. nov. for *Stenocephalus*, A. Schneider, 1875, preoccupied). Sporont oval, obese, with small conical protomerite. Cysts without sporoducts. Spores fusiform with a dark equatorial line. Unique species *S. juli* (Frantz.), from the digestive tract of millepedes, *Julus sabulosus* and *terrestris*, *Spirobolus marginatus*.

Family 4. Didymophyidae, Léger. Sporonts always associated in pairs, one behind the other, in such a way that the protomerite of the satellite disappears, and each syzygy resembles an individual with three chambers and two nuclei (Fig. 25, *a*).

Genus 31. *Didymophyes*, Stein, 1848. Epim. in form of a cylindro-conical spike (Fig. 25, *b*). Cysts dehiscing by simple rupture. Spores oval. *D. paradoxa*, St., from the intestine of *Geotrupes stercorarius;* and three other species.

Family 5. Dactylophoridae, Léger. Epimerite asymmetrical, irregular, bearing digitiform or root-like prolongations (Fig. 17, *h*, *i*). The dehiscence of the cysts is effected by simple rupture or by means of a pseudocyst (p. 183) placed laterally. Spores elongated, cylindrical (Fig. 34, *b*).

Genus 32. *Rhopalonia*, Léger, 1893. Epim. a subspherical knob bearing flexible digitiform processes. Trophozoites solitary, the conical body not septate, but with an indication of the protomerite. Unique species *R. geophili*, Lég., from digestive tract of *Geophilidae* and of *Stigmatogaster gracilis*. Genus 33. *Echinomera*, Labbé, 1899 (nom. nov. for *Echinocephalus*, A. Schneider, 1875). Trophozoite of oval or subconical contour, massive ; epim. persistent, spiked, the point furnished with small digitiform appendages which are not persistent, the whole forming with the protomerite a cone with summit displaced and slightly excentric (Fig. 17, *h*). Cyst dehiscing by simple rupture. Spores cylindrical with rounded bases, usually in strings (Fig. 34, *b*). Unique species *E. hispida* (A. Schn.), from the gut of *Lithobius forficatus*. Genus 34. *Trichorhynchus*, A. Schneider, 1882. Cephalont with cylindrical or truncated protom., bearing an elongated conical rostrum. Cysts oblong with wart-like eminences ; dehiscence by means of a lateral pseudocyst. Spores cylindrical or ellipsoidal, not in strings. Unique species *T. pulcher*, A. Schn., from the digestive tract of *Scutigera*. Genus 35. *Pterocephalus*, A. Schneider, 1887. Trophozoite with bilaterally symmetrical protom., divided into two lobes bearing spines or root-like processes, the two lobes united at one of their extremities to form a coiled horn (Fig. 17, *i*). Spores oval in form, connected obliquely into strings. Unique species *P. nobilis*, A. Schn., from the gut of *Scolopendra* spp. Genus 36. *Dactylophorus*, Balbiani, 1889. Protom. expanded excentrically, and carrying the digitiform processes of the epim. Sporonts solitary, of elongated form. Cysts dehiscing by means of a lateral pseudocyst. Spores cylindrical. Unique species *D. robustus*, Lég., from the gut of *Cryptops hortensis*.

Family 6. Actinocephalidae, Léger. Sporonts always solitary ; epim. symmetrical, simple or with appendages. Cysts dehiscing by simple rupture. Spores navicular, biconical, or cylindrical with conical extremities (Fig. 34, *d*). Parasitic for the most part in the guts of carnivorous Arthropods.

(1) SUB-FAMILY SCIADOPHORINAE, Labbé. Protom. umbrella-shaped, with radiating ridges terminating posteriorly in recurved spines. Spores biconical, the epispore with equatorial, the endospore with polar, dehiscence.

Genus 37. *Sciadophora*, Labbé, 1899 (nom. nov. for *Lycosella*, Léger, 1896, preoccupied), with the characters of the sub-family. *S. phalangii* (Lég.), from the gut of *Phalangium crassum* and *P. cornutum ;* two other species, also from *Phalangidae.*

(2) SUB-FAMILY ANTHORHYNCHINAE, Labbé. Spores ovoid with pointed ends, joined in strings by an equatorial suture.

Genus 38. *Anthorhynchus*, Labbé, 1899 (nom. nov. for *Anthocephalus*, A. Schneider, 1887). Epim. a large grooved knob. Unique species *A. sophiae* (A. Schn.), from the gut of *Phalangium opilio.*

(3) SUB-FAMILY PILEOCEPHALINAE, Labbé. Epim. simple, conical, or lance-like. Spores usually biconical.

Genus 39. *Pileocephalus*, A. Schneider, 1875. Epim. shaped like a lance-head (Fig. 17, *c*). *P. heerii* (Köll.), from the gut of Phryganid larvae and *P. chinensis*, A. Schn., from the gut of Mystacid larvae ; two other doubtful species. Genus 40. *Amphoroides*, Labbé, 1899 (nom. nov. for *Amphorella*, Léger, 1892, preoccupied). Epim. spiked or globular; sporonts solitary ; protom. very short, compressed, hollowed out into a cup. Spores biconical. Unique species, *A. polydesmi* (Lég.), from the gut of *Polydesmus complanatus.* Genus 41. *Discorhynchus*, Labbé, 1899 (nom. nov. for *Discocephalus*, Léger, 1892, preoccupied). Epim. large, in the form of boss surrounded by a thick ring ; protom. globular, larger than the deutom. Spores biconical, obese. Unique species, *D. truncatus* (Lég.), from the gut of *Sericostoma* sp., larva.

(4) SUB-FAMILY STICTOSPORINAE, Labbé. Spores biconical, with slightly curved, pointed terminations ; the endospore with numerous little papilliform elevations.

Genus 42. *Stictospora*, Léger, 1893. Epim. with a globular head, depressed ventrally and covered with projecting ribs terminating posteriorly in spikes. Spores biconical, the points slightly curved inwards. Unique species, *S. provincialis*, Lég., from the gut of the larva of *Melolontha* and *Rhizotrogus.*

(5) SUB-FAMILY ACTINOCEPHALINAE, Labbé. Epim. with appendages (except in *Stylocystis*). Spores symmetrical, navicular, biconical, or cylindrical with pointed ends.

Genus 43. *Schneideria*, Léger, 1892. Trophozoite non-septate ; epim. a thick plate bordered by a rim composed of rib-like thickenings (Fig. 18). Spores smooth, obese, biconical. *S. mucronata*, Lég., from the larva of *Bibio marci*, and *S. caudata* (Sieb.), from the larva of *Sciara nitidicollis.* Genus 44. *Stylocystis*, Léger, 1899. Trophozoite non-septate; epim. in the form of a pointed bristle or sharp spine, usually curved. Sporonts solitary. Spores biconical. Unique species *S. praecox*, Léger, from the gut of the larva of *Tanypus* sp. (Diptera). While evidently closely allied to the foregoing genus, the epimerite lacks the appendages characteristic of the sub-family, and from the morphological point of view is intermediate between the simple epimerite of *Doliocystidae* and the more complex epimerites of *Actinocephalidae* (Léger). Genus 45. *Asterophora*, Léger, 1892. Epim. composed of a circular ridge with radiating rib-like thickenings, surrounding a prominent central papilla. Protom. ordinarily larger than the deutom. Sporonts solitary, of elongated form. Spores cylindrical with conical extremities. *A. mucronata*, Lég., from the gut of the larva of *Rhyacophila*, and *A. elegans*, Lég., from the digestive tract of the larvae of *Phryganea grandis* and *Sericostoma* sp. Genus 46. *Stephanophora*, Léger, 1892. Epim. large, in form of a convex disc bearing a crown of finger-shaped tentacles. Spores as in the last. Unique species *S. lucani* (Stein), from the gut of *Dorcus parallelipipedus*. Genus 47. *Bothriopsis*, A. Schneider, 1875. Epim. in form of a lenticular knob bearing long flexible non-motile filaments. Sporonts solitary, with protom. greatly developed and very mobile. Spores biconical, obese. Unique species *B. histrio*, A. Schn., from the gut of *Hydaticus* sp. Genus 48. *Coleorhynchus*, Labbé, 1899 (nom. nov. for *Coleophora*, A. Schneider, 1885, preoccupied). Sporont with protom. in the form of a sucker or strawberry, extending over the deutom.; septum convex, projecting into the protom.; deutom. subspherical or cylindrical. Spores navicular. Unique species *C. heros* (A. Schn.), from the gut of *Nepa cinerea*. Genus 49. *Légeria*, Labbé, 1899 (nom. nov. for *Dufouria*, A. Schneider, 1875). Protom. dilated, club-shaped; septum convex, projecting into protom. Spores subnavicular, with thick sporocysts. Unique species *L. agilis* (A. Schn.), gut of larva of *Colymbetes* sp. Genus 50. *Phialoides*, Labbé, 1899 (nom. nov. for *Phialis*, Léger, 1892, preoccupied). Epim. in the form of a retractile boss, surrounded by a circular ridge and a collar-like membrane with pleats terminated by triangular teeth. Sporonts massive, solitary. Spores biconical, obese. Unique species *P. ornata* (Lég.), from the gut of the larva of *Hydrophilus piceus*. Genus 51. *Geneiorhynchus*, A. Schneider, 1875. Epim. in the form of a disc bristling with fine pointed teeth, carried on a very elongated neck (Fig. 17, *g*). Spores subnavicular. Unique species *G. monnieri*, A. Schn., from the gut of the nymph of *Libellula*. Genus 52. *Actinocephalus*, Stein, 1848.[1] Epim. sessile or on a well-marked neck, and provided with hooks or spines. Spores biconical. *A. stelliformis*, A. Schn., from the gut of *Ocypus olens* and other beetles; and other species. Genus 53. *Pyxinia*, Hammerschmidt, 1838. Epim. in the form of a cup or saucer with fringed rim surrounding a central spike (Fig. 15). *P. rubecula*, Hamm. (Figg. 15 and 33), from the gut of *Dermestes lardarius* and *D. vulpinus*; and other species. Genus 54. *Beloides*, Labbé, 1899 (nom. nov. for *Xiphorhynchus*, Léger, 1892). Epim. in form of disc or knob furnished with about ten teeth, and bearing in the centre a long spike (Fig. 17, *e*). Spores elongate-oval or boat-shaped. *B. firmus* (Lég.), (Fig. 17, *e*), and *B. tenuis* (Lég.), both from the intestines of larvae of *Dermestes* spp.

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[1] The two species mentioned by Stein (Müller's *Archiv*, 1848) under the genus *Actinocephalus* were *A. acus*, Stein, from *Carabus glabratus* and *A. lucani* from *Lucanus* (*Dorcus*) *parallelipipedus*. The former of these is not mentioned in Labbé's Sporozoa, the latter is placed, following Léger, under the genus *Stephanophora*, Léger. These facts may necessitate a revision of the nomenclature of the genera of *Actinocephalidae*, since the genus *Actinocephalus* in *Das Thierreich* does not contain either of the species placed in it by the founder of the genus.

Family 7. Acanthosporidae, Léger. Sporonts always solitary. Epim. symmetrical, simple or with appendages. Cysts dehiscing by simple rupture. Spores garnished with bristles at the poles or equator (Fig. 34, *e*). Parasites of carnivorous insects.

Genus 55. *Corycella*, Léger, 1892. Protom. spherical, more or less dilated; epim. in form of a knob bearing a crown of eight large hooks (Fig. 16). Unique species *C. armata*, Lég., from the gut of *Gyrinus natator*, larva. Genus 56. *Acanthospora*, Léger, 1892. Sporonts solitary, of elongate oval form. Epim. in form of a conical obtuse knob. Spores oval, with a tuft of four bristles at each pole and an equatorial circlet of sharp spines. *A. pileata*, Lég., from the gut of *Omoplus* sp., larva, and two other species. Genus 57. *Ancyrophora*, Léger, 1892. Sporonts solitary, the posterior end pointed. Epim. a knob bearing flexible or rigid appendages in the form of recurved hooks. Spores biconical, with polar tufts and six equatorial bristles (Fig. 34, *e*). *A. gracilis*, Lég., from *Carabus auratus*, *C. violaceus*, and *Silpha thoracica*; *A. uncinata*, Lég., from the larvae of *Dytiscus*, *Colymbetes*, *Sericostoma*, and *Limnophilus rhombicus*. Genus 58. *Cometoides*, Labbé, 1899 (nom. nov. for *Pogonites*, Léger, 1892, preoccupied). Epim. a spherical knob, flattened centrally, bearing a circlet of flexible slender filaments (Fig. 17, *f*). Spores with a tuft of bristles at each pole and two circlets of equatorial bristles. *C. crinitus* (Lég.), from *Hydrobius*, larva; *C. capitatus* (Lég.), from *Hydrous*, larva, gut.

Family 8. Menosporidae, Léger. Sporonts solitary. Epim. symmetrical, with appendages, and connected to protom. by a long neck. Cysts spherical, dehiscing by simple rupture. Spores in the form of crescents more or less curved (Fig. 34, *g*). Parasites of larvae of *Agrionidae*.

Genus 59. *Menospora*, Léger, 1892. Epim. in form of a cup bordered by hooks. Unique species, *M. polyacantha*, Lég., from gut of *Agrion puella*, larva. Genus 60. *Hoplorhynchus*, Carus, 1863. Epim. in form of a disc bordered by sharp teeth. Unique species, *H. oligacanthus* (Sieb.), (Fig. 43), from gut of *Calopteryx virgo*, larva.

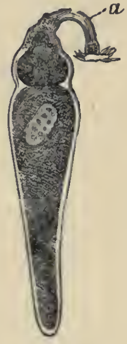

Fig. 43.

*Hoplorhynchus oligacanthus* (Sieb.), from the larva of *Calopteryx*. (From Lankester.)

Family 9. Stylorhynchidae, A. Schneider. Tropho. with body usually elongated, and epim. symmetrical, with or without appendages. Cysts with two envelopes closely joined; dehiscence by means of pseudocyst. Spores pouch-like, brown or blackish, joined in strings, and dehiscing by a split corresponding to the most convex border (Fig. 34, *f*).

Genus 61. *Lophocephalus*, Labbé, 1899 (nom. nov. for *Lophorhynchus*, A. Schneider, 1882, preoccupied). Epim. sessile, hollowed into a cup bordered by a membranous rim with vesicular appendages. Protom. depressed. Cysts irregular, subspherical with areolar eminences. Unique species, *L. insignis* (A. Schn.), from gut of *Helops striatus* (Fig. 44). Genus 62. *Cystocephalus*, A. Schneider, 1886. Epim. vesicular, with short narrow neck. Unique species, *C. algierianus*, A. Schn., from the gut of *Pimelia* sp. Genus 63. *Oocephalus*, A. Schneider, 1886. Epim. in the form of a rounded knob carried by a short conical neck. Unique species *O. hispanus*, A. Schn., from the gut of *Morica* sp. Genus 64. *Sphaerorhynchus*, Labbé, 1899 (nom. nov. for *Sphaerocephalus*, A. Schneider, 1886). Epim. small, spherical or oval, borne on a long, broad cylindrical neck, sharply constricted below the epim. Unique species *S. ophioides* (A. Schn.), from the gut of *Akis*. Genus 65. *Stylorhynchus*, Stein, 1848. The protom. of the cephalont is prolonged into a cylindrical, elongated rostrum, carrying at its termination the small knob-shaped epim. (Fig. 17, *d*); protom. of the sporont rounded; the deutom. very elongated. *S. longicollis*, Stein, from the gut of *Blaps mortisaga* (Fig. 45); and other species.

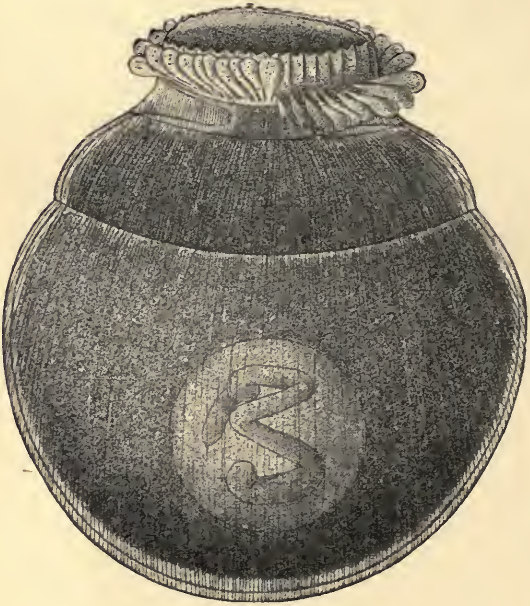

Fig. 44.

*Lophocephalus insignis* (A. Schn.), (par. *Helops striatus*), showing the large epimerite and the nucleus with a band-shaped karyosome. (From Wasielewski, after Léger.)

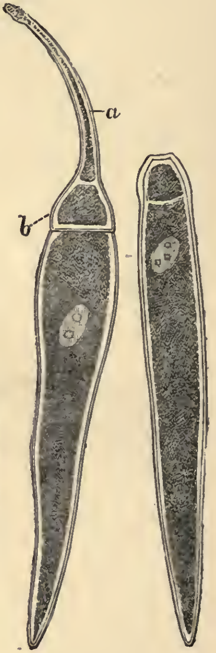

Fig. 45.

*Stylorhynchus longicollis*, Stein (par. *Blaps mortisaga*). On the left a cephalont, with a long epimerite (*a*) attached to the protomerite (*b*). On the right a sporont, the epimerite having been cast off. (From Lankester.)

Family 10. Doliocystidae. Epim. symmetrical, simple. Body non-septate. Spores oval. Parasites of marine Annelids.

Genus 66. *Doliocystis*, Léger, 1893. Body showing no trace of protom. or septum. Spores oval, with a thickening of the sporocyst at one pole. *D. pellucida* (Köll.), from the gut of *Nereis cultrifera* and

*N. beaucoudrayi; D. aphroditae* (Lank.), from the gut of *Aphrodite* (Fig. 19); and other species.

The following genera of Cephalina are of uncertain position :—

Genus 67. *Nematoides*, Mingazzini, 1891. Trophozoite vermiform, without septum ; epim. in form of a fork or pair of pincers, borne on an elongated neck. Unique species *N. fusiformis*, Ming., from the gut of *Balanus perforatus* and *Pollicipes cornucopia.* Genus 68. *Ulivina*, Mingazzini, 1891. Body of elliptical form, protom. a quarter the length of the body. The external membrane forms a continuous sac round the animal. *U. elliptica*, Ming., from the gut of *Audouinia filigera.* Genus 69. *Sycia*, Léger, 1892. Epim. knobbed, bordered by a thick ring (Fig. 17, *b*). Protom. subspherical ; deutom. conical ; with numerous enclosures. *S. inopinata*,

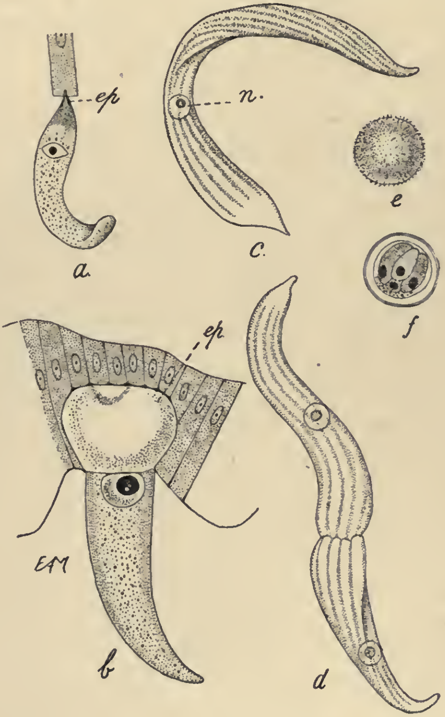

Fig. 46.

*Selenidium*, various species. *a*, comma-shaped species ("*Selenidium* en virgule") from *Cirratulus cirratus*; *ep*, minute epimerite, afterwards thrown off. *b*, semicolon-like species ("*S.* en point et virgule") from the same host, with very large epimerite. *c-f*, stages of *S. echinatum*, C. and M. (par *Dodecaceria concharum*). *c*, free sporont; *d*, syzygy of two sporonts; *e*, a spore, external view, showing the spiny surface; *f*, a spore in section, showing the four sporozoites. *a* and *b*, × 500; *c* and *d*, × 300; *e* and *f*, × 850. (After Caullery and Mesnil.)

Lég., from the gut of *Audouinia* sp. Genus 70. *Selenidium*, Giard, 1884, emend. Caullery et Mesnil, 1899, incl. *Esarhabdina*, Mingazzini, 1891, *Polyrhabdina*, Ming., 1891, and *Platycystis*, Léger, 1892. Body attenuated, vermiform, without septum, showing longitudinal striations due to myocyte fibrillae at the surface. Epimerite slender, conical, or large and globular (Fig. 46, *a*, *b*). Spores spherical, spined, and exceptional amongst Gregarines in being tetrazoic (Fig. 46, *e*, *f*). Parasites of Polychaetes. Type *S. pendula*, Giard, from the body-cavity of *Nerine; S. echinatum*, C. et M., from the gut of *Dodecaceria concharum;* other species from *Scololepis fuliginosa*, *Cirrhatulus cirratus*, and other marine Annelids. See especially Caullery and Mesnil [8*b*].

## ORDER 2. **Coccidiidea**

The Coccidiidea are an order of the *Telosporidia* (p. 166), characterised by the following distinctive features. They are cell-parasites, attacking tissue-cells, and especially epithelial cells, rarely other forms of tissue, and never blood-cells. The trophozoite grows within the infected cell into an oval or spherical body, with great resemblance to an ovum; it is quite motionless, never at any period amoeboid, and remains intracellular during at least the whole trophic stage. The dissemination of the parasite is always accomplished by means of resistent *oöcysts*, the formation of which is preceded by the conjugation of differentiated gametes in all cases that have been thoroughly investigated. Within the oöcyst the zygote breaks up into sporoblasts (*archispores*), which either become converted into naked sporozoites (*gymnospores*), or into spores (*chlamydospores*), each containing from one to four sporozoites, seldom more. In addition to this exogenous method of reproduction, or *sporogony*, by means of durable cysts, the life-cycle is often complicated by endogenous multiplication, or *schizogony*, serving for the increase of the parasites within the host. The schizogony is not preceded by conjugation, and is not accompanied by formation of any oöcysts or sporocysts.

The Coccidia have attracted the attention of naturalists and medical men for a long time past, by their frequent occurrence in the rabbit and other Vertebrates, in which they may be present in such masses that their presence cannot fail to be detected by simple inspection when the host is dissected. Earlier observers often held, however, very erroneous views as to the nature of these parasites. Hake, who in 1839 was the first to describe Coccidia, regarded them as pathological products of the diseased animal—in fact, as a form of pus-corpuscles; and similar views were held by many subsequent writers. On the other hand, a number of authorities in the forties and fifties believed Coccidia to be eggs of parasitic worms. Remak, in 1845, was the first to point out their relations to Müller's "psorosperms," and in 1854 Lieberkühn insisted upon their affinities with Gregarines. A year later Kloss gave the first thorough account of the life-cycle, in the case of the form infesting the snail, subsequently named *Klossia helicina* by A. Schneider. Kloss's work was also the first proof of the existence of these parasites in Invertebrates. The endogenous life-cycle was first described by Eimer in 1870, in the form infesting the mouse, termed by him *Gregarina falciformis;* but later (1875) made by Schneider the type of a new genus, *Eimeria.* Henceforth these organisms became known as "egg-shaped psorosperms" (eiförmige Psorospermien, Psorospermies oviformes), and their affinities with the Gregarines received general recognition. In 1879 Leuckart greatly increased our knowledge of the Coccidian parasites of the rabbit, and introduced for them the new generic name *Coccidium*, in the second edition of his well-known treatise upon human parasites. From this time onwards these parasites were commonly known as "Coccidia"—a word often used in an extremely vague sense by writers whose zoological knowledge is defective, and by whom it is sometimes employed in a sense practically synonymous with the older word "psorosperms."

In the eighties our knowledge of the forms of Coccidia and their life cycles was steadily increased, chiefly by the labours of Aimé Schneider, and in more recent years by Labbé. In the last decade of the nineteenth century a vast amount has been written about Coccidia on account of the connection suspected to exist between them and cancer, but this work has been for the most part barren of results, contributing little to extend our knowledge either of cancer or of Coccidia. It is in this period, however, that the complete life-cycle has been gradually worked out by a number of observers. An alternation of generations was first suggested by L. and R. Pfeiffer, whose ideas met with the most vigorous criticism, but a double life-cycle has now been demonstrated to be of almost universal occurrence amongst Coccidia. Towards the end of the nineteenth century, also, sexual reproduction has been observed and accurately studied in a number of forms. The new century commences with an exhaustive monograph by Schaudinn upon the complete life-history of the forms infesting the centipede *Lithobius*, a publication which marks an epoch in the investigation not only of Coccidia but of Sporozoa generally, and completes our knowledge of a most fascinating chapter in natural history.

(*a*) *Occurrence, Habitat, Effects on their Hosts, etc.*—The Coccidia are an abundant group of the Sporozoa, but appear to be confined, in the matter of hosts, to three great phyla—the Arthropoda, Mollusca, and Vertebrata.[1] In the last named they are found more commonly than any other Sporozoa, and have long been familiar on account of their frequent occurrence amongst domestic animals, both in birds and mammals, and even in man. They are met with in all the five classes of Vertebrates more or less commonly, and the very numerous species of the type-genus *Coccidium* are almost confined to Vertebrate hosts.[1] In Mollusca, Coccidian parasites are very common in Gastropoda and Cephalopoda, and *Hyaloklossia pelseneeri*, Léger, occurs in the kidneys of the Lamellibranch *Tellina;* a species, of position as yet doubtful, occurring also in the kidneys of *Donax* (Léger [41]). In Arthropods, Coccidia occur sparingly in Insects, more abundantly in Myriapods, but have not been found as yet in either Arachnida or Crustacea.

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[1] Exceptions are the Coccidian parasites discovered by Caullery and Mesnil in the gut of *Capitella capitata* [126] and other Polychaete worms [129a]. Since only the schizogony was observed, the systematic position of these forms could not be determined; they remain for the present, therefore, without any generic or specific designation. On the other hand, these authors are of opinion that the alleged Coccidian parasites in *Perichaeta*, described by Beddard (*Ann. Mag. Nat. Hist.* (6), ii. 1888, p. 433), are nothing more than segmenting eggs of Nematodes. It is

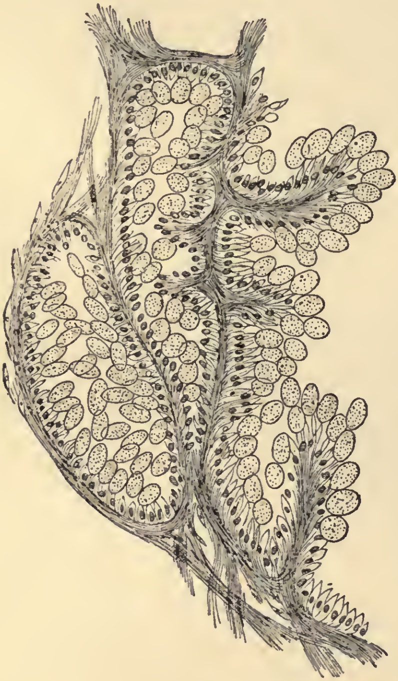

Fig. 47.

Section of rabbit's liver infected with *Coccidium oviforme*, Leuck. After Balbiani, from Wasielewski.

The Coccidia are chiefly parasites of epithelial cells, and since the infection of the host appears to take place in all cases by way of the digestive tract, it is the epithelium of the gut or of its appendages, such as the liver (Fig. 47), that is most often the seat of the parasite. In a considerable number of cases, however, the parasitic germs, after entering the system by way of the gut, go further afield before settling down. Passing through the gut-wall, the parasites are transported, probably, by the circulation of the blood or lymph, to their specific habitat. In those cases in which the vascular system forms the general body-cavity (haemocoele), we find occasionally, though very rarely, what is so common in the Gregarines, namely, Coccidia as "coelomic" parasites.[2]

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possible that some of the supposed Coccidia seen in Polychaeta are really intracellular stages of Gregarines; but a genuine Coccidian, *Caryotropha mesnilii* (Fig. 67) has recently been described by Siedlecki [55*a*] from *Polymnia nebulosa*.

[1] Exceptions are two species found in *Lithobius forficatus*, viz. *Coccidium lacazei* (Labbé), and *C. schubergi*, Schaudinn.

[2] An example is *Adelea mesnili*, Perez, 1899 [50], from the body-cavity of

As a general rule, however, the parasite selects some particular organ, most often the excretory organs.[1] In Molluscs, especially, the kidneys are the seat of these parasites more often than any other organ (Fig. 48). In Arthropods this is less frequently the case, but *Eimeria nova*, A. Schn., is found in the Malpighian tubules of *Glomeris*. In Vertebrates again the kidney is very often attacked; in other cases amongst this phylum it is not infrequently the spleen, and even in a few instances the testis, which is selected by Coccidian parasites—never, however, the ovary; so that in this

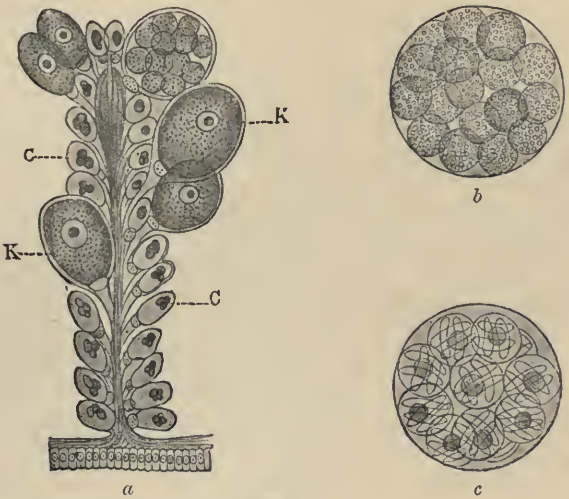

FIG. 48.

*Klossia helicina*, A. Schn., from the kidney of *Helix hortensis*, after Balbiani, from Wasielewski. *a*, portion of a section of the kidney, showing normal epithelial cells containing concretions (*C*), and enlarged epithelial cells containing the parasite (*K*) in various stages. *b*, cyst of the *Klossia* containing sporoblasts. *c*, cyst with ripe spores, each enclosing four sporozoites and a patch of residual protoplasm.

the moth *Tineola biseliella*; it attacks chiefly the fat-body, but may overrun also the pericardial cells, oenocytes, Malpighian tubules, muscles, and epidermis; it is never found, however, in the gut-epithelium, nor does it penetrate the nervous system, gonads, or imaginal discs. Another example is *Adelea akidium*, Léger, parasitic upon various beetles (*Akis* spp.; *Olocrates abbreviatus*); it also attacks the fat-body and the pericardial cells, but not any other organs.

[1] With regard to the question of the transport of the parasites within the body of the host, Laveran [35] has drawn attention to an association between *Coccidium metchnikovi*, Lav., and a Myxosporidian, *Myxobolus oviformis*, Thél., in the gudgeon. The *Myxobolus* in the liver, spleen, and kidney is found containing the *Coccidium* in various phases of development, especially in the stage of cysts with spores, in which case the *Myxobolus* usually contains no spores of its own. Free Coccidia not contained in Myxosporidia are found only in the intestine. Laveran believes that the Coccidia penetrate the Myxosporidia in the intestine, and that the latter then invade the organs they affect, and transport the Coccidia with them. This view is contested by Blanchard ([30], p. 161).

respect the predilections of Coccidia are the opposite of those of Myxosporidia, which frequently attack the ovary but never the testis. A given species of Coccidian parasite may confine its attentions entirely to some particular organ, or it may attack several organs, as for example *Coccidium minutum*, Thél., found in the liver, spleen, and kidney of the tench; but as a rule it is rare for a form infesting the epithelium of the digestive tract to attack other internal organs as well.

Coccidia during the trophic stage are always intracellular parasites,[1] and each trophozoite destroys completely the cell which harbours it. As a rule the trophozoite lies in the cytoplasm and does not attack the nucleus directly, but pushes it to one side, often indenting or compressing it. The first effect of the extranuclear parasite is to produce a considerable hypertrophy of the host-cell, especially of its nucleus. The cell is stimulated to increased metabolism, shown not only in rapid growth, but also in the formation by it of fatty substances, which serve as nutriment for the parasite and are consumed by it (Schaudinn [51]). The effects of the parasite are not confined to the cell which harbours it, but may extend to the surrounding tissues; in *Helix hortensis* attacked by *Klossia helicina* the neighbouring epithelial cells of the kidney are stimulated to karyokinesis and multiplication, and a proliferation of the cells of the connective tissue is induced, leading to the formation of a fibrous envelope round the masses of Coccidia as a healing process on the part of the host (Laveran [38]). Ultimately, however, the infected cell is so weakened that it can no longer assimilate, but dies and is finally absorbed by the parasite, only a compact lump of chromatin and a small quantity of protoplasm remaining. The parasite then passes into the reproductive stage, either still enclosed by the remnants of the cell it has destroyed, in schizogony, or freed from the cell, in sporogony.

A certain number of Coccidia occur, on the other hand, as intranuclear parasites. The schizogonous generations of certain species of *Coccidium* occurring in Amphibia (frog, salamander, newt) commonly attack the nucleus itself of the infected cell, and have hence been described by Steinhaus under the generic name *Karyophagus*. The recently described *Cyclospora caryolytica*, Schaud., parasite of the intestinal epithelium of the mole, owes its specific name also to its intranuclear habitat, which in this case seems to be an invariable characteristic of the parasite. The effects of this intranuclear parasitism have recently been studied by Schaudinn [51*a*] and Dormoy [33], and are seen chiefly in an enlargement of the nucleus, accompanied by absorption of its contents. The linin framework is broken up, vacuoles are formed in it, and the chromatin fuses into irregular lumps and strands. The nucleus becomes enlarged to six or even ten times its normal diameter by absorption of fluid from the cell. The chromatic substance is forced out, by growth of the parasite, to the periphery of the nucleus, and ultimately disappears, so that "the entire nucleus is transformed into a gigantic vacuole, in the interior of which the parasite floats" (Schaudinn). The cytoplasm of the cell, on the other hand, is absorbed and shrivels up rapidly as the nucleus enlarges, without going through any stage of hypertrophy such as results from extranuclear parasitism.

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[1] Very recently Laveran and Mesnil have described a species under the name *Coccidium mitrarium* (see p. 233), which, according to these authors, is unique amongst Coccidia in having an extracellular development like a Gregarine.

Each individual trophozoite in this way brings about the destruction of a cell, but of one only, in its host. Nevertheless, the parasites are often present in such vast numbers that the epithelium of the organ affected may be completely destroyed, and the host itself killed or reduced to the last extremity. In centipedes experimented upon by Schaudinn, the faeces became milk-white during the acute stage of the Coccidiosis, and consisted entirely of epithelial remains and Coccidian cysts. The intestine may be so stripped of its epithelium that the young sporozoites are unable to find an epithelial cell to infect, in which case they may attack a full-grown Coccidian of another species, but never of their own kind (Schaudinn [51]). In the mole, *Cyclospora caryolytica* is the cause of a pernicious form of enteritis accompanied by violent diarrhœa, which is generally fatal to the host (Schaudinn [51*a*]). In rabbits young animals are often killed by the attacks of Coccidia infesting the epithelium of the bile-ducts, and similar cases are known in the human species.[1] The liver is greatly enlarged, and its blood-vessels compressed, leading to functional derangements; the secretion of bile is reduced to a minimum; the blood becomes pale and watery, as in pernicious anaemia; the respiration becomes gasping, and the animal finally dies in convulsions. In all these cases the destructive power of the parasite varies directly as its power of multiplying by schizogony, and so overrunning the tissues which it attacks; and it is a very interesting and important fact, that in no case, apparently, can the schizogony continue indefinitely, but has its own natural, intrinsic limit, after which conjugation, with consequent sporogony, is necessary for the recuperation of the parasite and the continuance of its race. If, therefore, the patient can safely pass the acute stage, the disease heals itself through the failing reproductive powers of the parasite, on the one hand, and the regenerative capacity of the epithelium on the other. The injury inflicted on the host is repaired more or less completely;

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[1] For a full account of the pathology of Coccidiosis, with special reference to man, see Blanchard [30].

but the patient is by no means immune against the consequences of a fresh infection from without.

In other Coccidia the schizogony may be wanting altogether, or be more limited in its duration, and in such cases the parasites are very harmless and inflict little or no injury upon their hosts. This is especially true of those found in Mollusca, commonly infesting, as has been said, the kidneys in these animals.

(*b*) *Morphology and Evolution.*—The complete life-cycle of *Coccidium schubergi* has been worked out so thoroughly and in such detail by Schaudinn, that it may serve very well as a type of the whole order, the chief variations that are known to occur being specified afterwards.[1]

*Coccidium schubergi* is parasitic in the intestinal epithelium of *Lithobius forficatus*, where it is commonly found in company with two other species, *Coccidium lacazei* (Labbé), and *Adelea ovata*, A. Schn. The infection of the centipede is started by its accidentally swallowing cysts with its food. The cyst-wall is then dissolved by the digestive fluids, the four spores each split lengthways, and the sporozoites, of which two are contained in each spore, are liberated in the digestive tract. Each sporozoite proceeds at once to attack, and to penetrate within, an epithelial cell of the host.

The free sporozoite is a minute, sickle-shaped body 15-20 $\mu$ in length, 4-6 $\mu$ in breadth (Fig. 49, *a* and *b*, and Fig. 50, *a*). The anterior extremity is more pointed and refringent, the posterior end more rounded. The finely-granulated protoplasm, which is not limited by any distinct cuticle, contains a spherical nucleus placed near the middle of the body, visible in life as a clear spot, and showing after preservation and staining a number of chromatin granules, lodged in an alveolar linin framework, *but no special central corpuscle, nucleolus, or karyosome.* The sporozoite performs active movements of various kinds. In the first place, it changes its form, as a whole, either by bending the body like a bow, and then straightening it out again, or by ring-like constrictions of the body which run from the anterior to the posterior end in waves of contraction (Fig. 49, *e* and *f*), similar to the "euglenoid" movements of Gregarines and Flagellates (see p. 181). During these contractile movements a fine longitudinal striation of the body surface is to be observed, caused, however, not by the presence of myocyte-fibrillae, but by the arrangement of the superficial alveoli of the protoplasm in longitudinal rows (Schaudinn [51*a*]). In the second place, the sporozoite moves forward by a gliding movement similar to that of Gregarines, and effected in a similar manner, namely, by secretion of a gelatinous thread which pushes the little animal forward as it is formed (Fig. 49, *a* and *b*); movements of progression of this kind alternate with movements of flexion, and after having traversed from five to seven times its own length, it comes to a stop, bends its body three or four times, and starts again. Thus the sporozoite greatly resembles in its movements and general appearance a minute Gregarine.

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[1] In the following account of the life-histories of Coccidia, the terminology employed for the various stages is that which has been gradually evolved by numerous authors during recent years, and to which Schaudinn has put the finishing touches. The chief departures here from Schaudinn's nomenclature are, that the term "zygote" is used instead of "copula," and that the term "oöcyst" is understood to mean the membrane rather than the contents. In many recent memoirs some of these special terms are employed in different senses, making the descriptions often very difficult to understand. The commonest instance of this is the use of the term "macrogamete" to denote what should be termed a female merozoite or macromerozoite (see p. 223).

Some authors, amongst whom Lang and Grassi are especially prominent, make use of a quite different terminology, proposed originally by Haeckel. The non-sexual schizogony is termed *monogony*, as being a case of reproduction by *single* individuals, without conjugation, and the schizonts are termed *mononts.* The gametocytes are termed *gametogenous mononts*, the formation of the gametes being regarded as a special case of monogony. The zygotes or sporonts are termed *amphionts*, formed as they are by the coming together of *two* individuals, and the sporogony is termed *amphigony.*

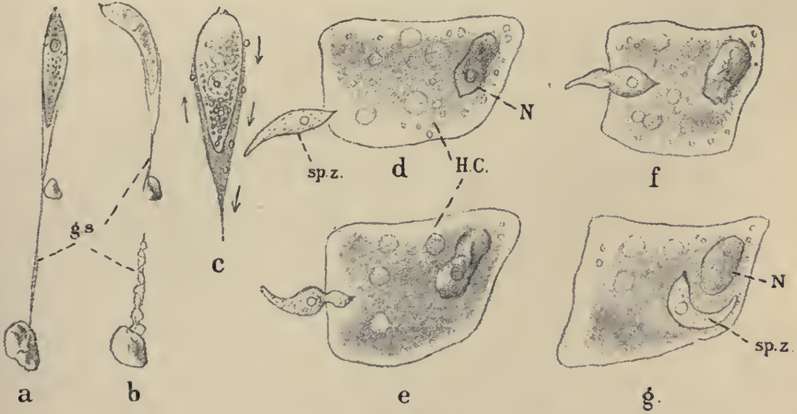


FIG. 49.

Movements of living sporozoites and merozoites of *Coccidium schubergi*, Schaud. (par. *Lithobius forficatus*). After Schaudinn [51]. *a*, *b*, forward progression of a sporozoite by secretion of a gelatinous thread (*g.s*), which is attached to foreign objects, and pushes the little creature forwards. In *b* the portion of the thread between two foreign bodies has snapped and shrivelled up. *c*, a merozoite in forward progression. The arrow on the left shows the direction in which the merozoite is moving; those on the right, the direction in which the gelatinous substance secreted by it is flowing backwards to form a filament. *d*-*g*, penetration of an epithelial cell by a sporozoite. *H.C*, host-cell; *N*, its nucleus; *sp.z*, sporozoite.

By means of its progression the sporozoite reaches an epithelial cell, and presses its anterior pointed end into it (Fig. 49, *d*). The opening is widened by its euglenoid contractions, and is still further increased by its movements of flexion and extension. In five or ten minutes it has worked its way into the cell (Fig. 49, *e*-*g*). Its movements then slowly cease, and it comes to rest near the nucleus, but sometimes a sporozoite traverses four or five epithelial cells before settling down.

Within the epithelial cell the sporozoite becomes a motionless oval body, which absorbs the fatty nutriment provided for it by the cell (see above, p. 208), without, however, forming any fat-granules in its own substance or laying up any kind of reserve nutriment. It grows rapidly, becoming in twenty-four hours a full-sized, spherical trophozoite. Most remarkable are the changes which take place in the nucleus during the growth of the trophozoite. Larger fragments of the chromatin, which was at first scattered evenly in the nuclear framework, collect gradually towards the centre of the nucleus, where they soon appear imbedded in a diffuse, feebly-refractile substance, apparently allied to plastin in nature (Fig. 50, *b*). The pieces of chromatin fuse with the plastin matrix to form a solid spherical body, homogeneous in appearance, except for a few vacuoles of nuclear sap (Fig. 50, *c*-*e*). The body thus formed resembles the nucleolus of Metazoan cells in its appearance and relations, but differs in containing chromatin. It has therefore received the distinctive name of *karyosome*. The karyosome lies towards the centre of the nucleus, or slightly excentrically. The rest of the nuclear framework retains its finely meshed condition, and lodges very minute chromatin-granules. The karyosome is retained through all the stages of schizogony, and its presence is absolutely distinctive of the schizogonous generations, but of them alone.

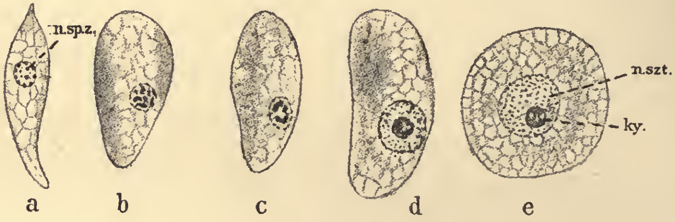


FIG. 50.

Development of a sporozoite into a schizont, showing the formation of the karyosome, in *Coccidium schubergi*, Schaud. (par. *Lithobius forficatus*). After Schaudinn [51]. *a*, sporozoite with a granular chromatic nucleus (*n.sp.z*) but no karyosome. *b*, larger granules of chromatin appear towards the centre of the nucleus. *c*, the larger granules become more concentrated. *d*, they become united by a ground-substance into a central corpuscle or karyosome. *e*, schizont, with a large nucleus (*n.szt*) containing the karyosome (*ky*).

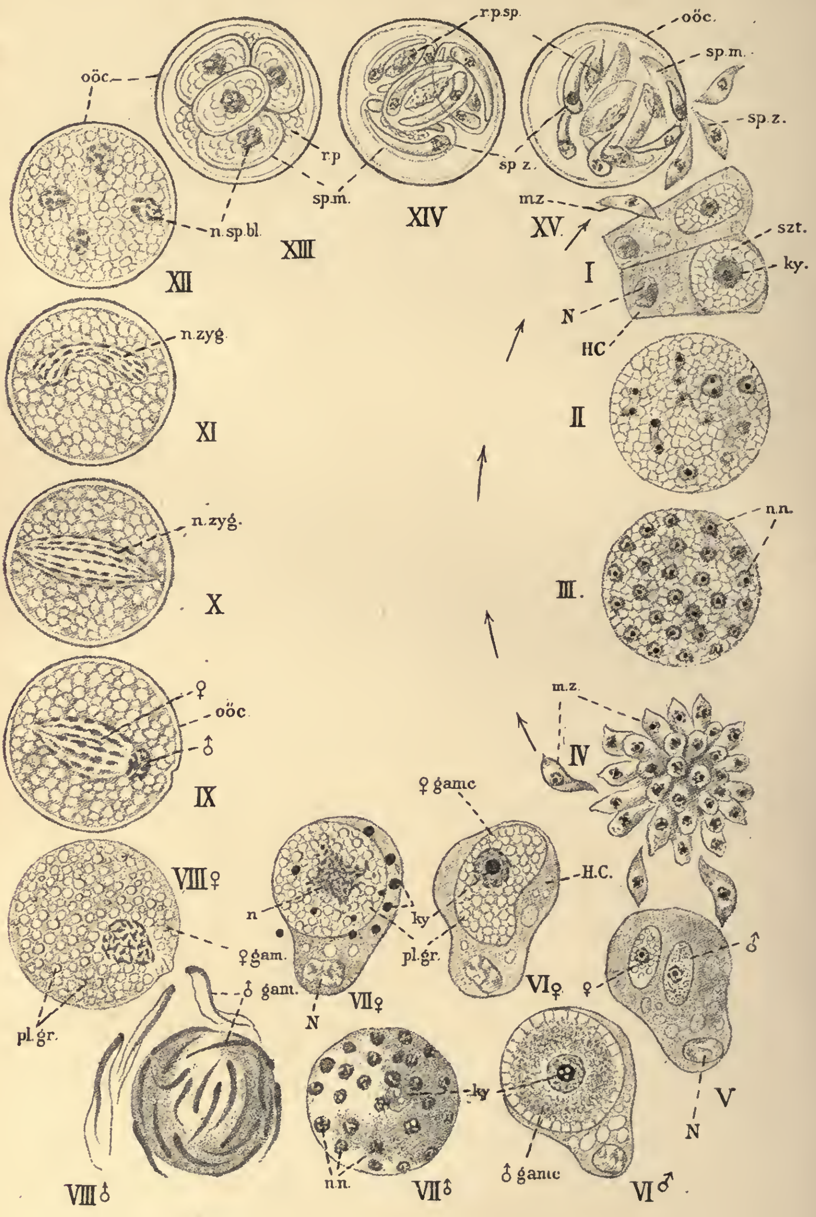
When the trophozoite is full-grown and has exhausted the host-cell, it proceeds to reproduce itself by *schizogony* (Fig. 51, I-IV), and is hence termed a *schizont*. The schizogony goes on within the host-cell, the withered remains of which form an envelope to the schizont, no cyst or protective membrane being formed by the parasite itself. The schizonts are distinguished by their coarsely alveolar or vacuolated protoplasm containing very few granular enclosures, if any. The nucleus of each schizont divides to form a number of daughter nuclei, which travel to the periphery and are scattered at more or less regular intervals at the surface of the cell-body. The protoplasm adjacent to each nucleus then commences to grow out and project above the surface of the schizont, taking the nucleus with it. Thus are formed a number of club-shaped bodies, each very similar to a sporozoite, but differing from it in certain points of structural detail as well as in origin, and hence distinguished as a *merozoite* (Figg. 51, IV, and 49, *c*). The parent schizont, which drops out of the host-cell at this stage, is not converted entirely into merozoites, but a certain amount of residual protoplasm is left, destined ultimately to be cast off and to die and break up.

The schizogony here described takes place in a similar manner in many Coccidia, and has been frequently observed since it was first described by Eimer for the *Coccidium falciforme* of the mouse in 1870; but until recently the connection between the different parts of the life-cycle were not understood, and the schizogonous generations were considered as representing a distinct generic type, to which A. Schneider in 1876 gave the name of *Eimeria.* Hence this portion of the life-history is often termed the Eimerian phase ("Cycle Eimerien").

The division of the nucleus of the schizont in the process of schizogony sketched above does not always follow the same method in all Coccidia, not even in the three species inhabiting *Lithobius.* In *Adelea ovata* and *Coccidium lacazei* it takes place by a multiple fragmentation of the nucleus and karyosome, the fragments coming together again at the periphery in patches to form daughter nuclei, each with a central karyosome. But in *C. schubergi* the nucleus divides by repeated binary fission (Fig. 52, *a-e*). The karyosome divides first in all cases, and then the chromatin forms two masses round each of the daughter karyosomes, which play a part in the division similar to that performed by the nucleolo-centrosome in *Euglena* and *Paramoeba.* The process is one more akin to direct nuclear division than to mitosis, and current descriptions, showing beautiful nuclear spindles, are inaccurate and imaginative (Siedlecki, Schaudinn). The number of merozoites formed is very variable, and is probably directly related to the nutrition furnished by the host-cell. Usually about thirty or forty, apparently, the number may sink as low as four. Simple binary fission of merozoites or schizonts never occurs, however, since in all cases of schizogony, however much reduced, there is always left a residuary mass of protoplasm on which the merozoites are implanted all round, if numerous, or only on one side, if few.

The merozoites, at first connected by a stalk with the residual protoplasm of the schizont, soon begin to exhibit active movements and wriggle themselves free. Each merozoite resembles a sporozoite in its movements and general appearance, and differs chiefly in being more club-shaped and *in possessing a distinct karyosome.* The merozoites proceed to seek out and to attack fresh epithelial cells, as did the sporozoites before them, and in a similar way each merozoite grows into a trophozoite which becomes a schizont, and breaks up in its turn into a fresh generation of merozoites.

In this way schizogony may proceed merrily for many generations, and the numbers of the parasite increase by geometrical


oöc.
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mz
XV
szt.
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I
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II
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IV
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♂
♂ gam.
N
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V
N
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VIII♂
VII♂
♂ gamc
VI♂

FIG. 51.

progression within the host, until almost the entire epithelium of the digestive tract may be destroyed. Sooner or later (in *C. schubergi* after about five days) a limit is reached both of the nutritive capacity of the host and of the reproductive power of the parasite. Schizogony is then replaced by sporogony, a process always initiated by the production of sexually differentiated conjugating individuals or gametes. Merozoites, descended from a long succession of maiden schizonts, infect epithelial cells and become trophozoites in the usual way, but instead of growing rapidly into ordinary schizonts like their parents, they grow much more slowly to become the mother cells of gametes, or *gametocytes*. Since, further, the gametes are differentiated into male elements or *microgametes*, and female elements or *macrogametes*, their mother cells must be distinguished further into *microgametocytes* and *macrogametocytes*, which differ in all stages of their development.

Fig. 51.

The life-cycle of *Coccidium schubergi*, Schaud. (par. *Lithobius forficatus*), represented in all its principal stages, combined into a single diagram, after Schaudinn [51]. I-IV represents the schizogony, commencing with infection of an epithelial cell by a sporozoite or merozoite. After stage IV the development may start again at stage I, as indicated by the arrows; or it may go on to the formation of gametocytes (V). V-VIII represent the sexual generation. The line of development, hitherto single (I-IV), becomes split into two lines—male (VI ♂, VII ♂, VIII ♂) and female (VI ♀, VII ♀, VIII ♀), culminating in the highly differentiated gametes. By conjugation these two lines are again united. IX, X show the formation of the zygote by fusion of the nuclei of the gametes. XI-XV, sporogony.

I, two epithelial cells showing the penetration of a merozoite and its growth into a schizont. *H.C*, host-cell; *N*, its nucleus; *mz*, merozoite. *szt*, schizont; *ky*, its conspicuous karyosome. II, the nucleus of the schizont is dividing up. III, schizont with numerous daughter nuclei (*n.n*), each with a conspicuous karyosome. IV, the schizont has segmented into numerous merozoites (*mz*), each with a karyosome in its nucleus, implanted on a central mass of residual protoplasm, which in the figure is hidden by the merozoites. V, a host-cell containing two young gametocytes. The microgametocyte (♂) has fine granulations; the macrogametocyte (♀) has coarse granules. VI ♀, a host-cell containing an immature female gametocyte (♀ *gamc*), characteristically bean-shaped, with plastinoid granules (*pl.gr*) in the cytoplasm, and a distinct karyosome (*ky*) in the nucleus. VII ♀, a female gametocyte undergoing maturation, still in the host-cell. The body has become spherical, the nucleus (*n*) irregular, and the karyosome has been expelled in fragments (*ky*). VIII ♀, mature macrogamete, freed from the host-cell, and sending a cone of reception towards an approaching microgamete (♂ *gam*). VI ♂, a host-cell containing a full-grown microgametocyte (♂ *gamc*), spherical, with no plastinoid granules, and with distinct karyosome (*ky*). Compare VI ♀. VII ♂, the nucleus of the microgametocyte has divided up to form a great number of daughter nuclei (*n.n*), leaving the karyosome (*ky*) at the centre of the body. VIII ♂, the nuclei of the last stage have become microgametes (♂ *gam*), each with two flagella, which are quitting the protoplasmic body of the gametocyte, and swimming to find a macrogamete. IX, the zygote surrounded by a tough membrane or oöcyst (*oöc*), and containing the female chromatin, which is taking the form of a spindle (♀), and the male chromatin in a compact lump (♂). X, the chromatin from the two sources is spread over a spindle-like figure (*n.zyg*), and no longer distinguishable as male or female. XI, the spindle-shaped nucleus of the zygote, having become compact (*n.zyg*), is dividing. XII, four daughter nuclei are formed, the nuclei of the sporoblasts (*n.sp.bl*). XIII, the four sporoblasts are segmented off from a small quantity of residual protoplasm, or "*réliquat kystal*" (*rp*). Each sporoblast has secreted a membrane, the sporocyst (*sp.m*). XIV, within each sporocyst the nucleus has divided, and the protoplasm is segmented into two sporozoites (*sp.z*), and a *réliquat sporal* (*rp.sp*). The *réliquat kystal* of the last stage is absorbed. XV, release of the sporozoites. An aperture is formed in the wall of the oöcyst (*oöc*), and the sporozoites (*sp.z*) pass out through it, having been liberated by bursting of the sporocysts (*sp.m*), which, with the *réliquats sporaux* (*rp.sp*), are left behind in the oöcyst.

The microgametocytes are characterised by their dense, minutely-reticular (alveolar) protoplasm, which is very finely and evenly granulated, and is poor in larger enclosures or reserve material (Fig. 51, VI ♂). When formation of microgametes commences, the chromatin in the nucleus increases, fine granules of this substance being given off from the karyosome into the linin framework. At the same time the outline of the nucleus becomes irregular and indistinct, and it soon begins to send out processes into the cytoplasm, forming paths along which the chromatin-granules wander out and travel towards the periphery of the body of the gametocyte. They reach ultimately the most superficial layer of protoplasmic alveoli, leaving the pallid karyosome, now almost deprived of chromatin, in solitary state at the centre of the body of the gametocyte. At first scattered evenly, the minute chromatin-granules soon collect together and become concentrated into patches disposed at more or less regular distances from one another over the surface of the cell (Fig. 51, VII ♂). In each patch the chromatin-granules draw more closely together and fuse into a dense mass of chromatin, which at first has the form of an irregular tangle, but soon becomes a compact lump of chromatin enclosing a single clear vacuole. The nuclei so formed become lengthened and drawn out so as to be first comma-shaped, and then elongated and filamentous in form (Fig. 51, VIII ♂); each nucleus bends upwards so as to project from the body of the gametocyte, enveloped in a sharply-limited zone of hyaline protoplasm, from which two flagella grow out; active movements are at once set up by the flagella; and finally the nucleus breaks loose with its protoplasmic envelope and flagella, and is set free from the gametocyte as the minute and extremely active microgamete, the male element in conjugation. The microgametes swim off and swarm away in quest of the macrogametes, leaving the body of the microgametocyte, which is not sensibly diminished in bulk by subtraction of the microgametes, and which, with the karyosome still in its heart, is abandoned as residual protoplasm, and soon breaks up and dies. It is evident that the formation of microgametes is nothing more than a peculiar type of schizogonous generation, which differs in certain points, both of method[1] and

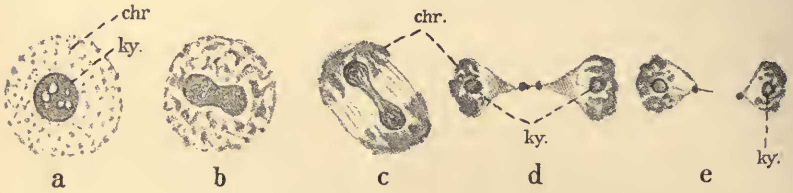

Fig. 52.

Division of the nucleus of the schizont of *Coccidium schubergi*, Schaud. (par. *Lithobius forficatus*), in schizogony. After Schaudinn [51]. *a*, resting nucleus, with karyosome (*ky*) and chromatin-granules (*chr*). *b*, the karyosome commences to divide. *c*, the karyosome forms a dumb-bell-shaped figure, round the two extremities of which the chromatin is aggregated. *d*, complete division of the karyosome, and separation of the chromatic portions of the nucleus. *e*, complete separation of the two daughter nuclei.

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[1] But the method is subject to variations in both cases, in Coccidia generally, and the difference between the formation of the microgametes and ordinary schizogony

result, from the ordinary pattern, and marks the full stop to reproduction by schizogony.

Each microgamete has a flexible, serpentine body, 6-7 $\mu$ in length by barely 1 $\mu$ breadth in *Coccidium schubergi* (Fig. 53, *a*, *b*, *d*, *e*). It may be extended at full length, or bent up into the form of a U by its own activity. The substance of the body consists principally of chromatin, which, however, contains the above-mentioned vacuole in its interior, and is itself enclosed in a delicate covering of protoplasm, from which spring the two flagella, one at each end of the body. At the extremity, which is anterior in movement, the protoplasmic envelope is more condensed to form a shining point or rostrum (*r*). From the base of the rostrum springs the anterior flagellum (*a.fl*), the chief agent in forward movement; it is very fine and slender, about twice the length of the body, planted on the side which is convex when the body is curved, and directed backwards. The posterior flagellum (*p.fl*) is a simple continuation of the hinder end of the body; it is shorter than the anterior one, and acts more as a rudder ("Schleppgeissel"). The microgamete as a whole thus bears a striking resemblance to the antherozoïd of a moss-plant.

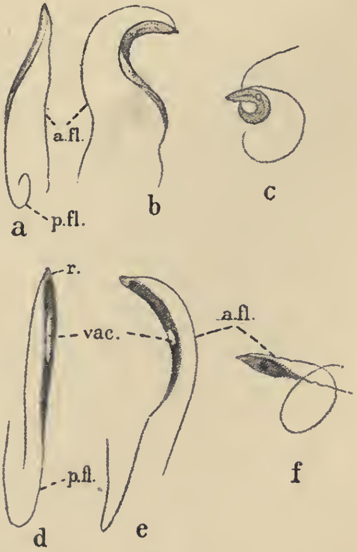

FIG. 53.

Microgametes of *Coccidium schubergi*, Schaud. (*a*, *b*, *d*, *e*), and *C. lacazei* (Labbé), (*c*, *f*). *a*, *b*, and *c* are drawn from the living objects; *d*, *e*, and *f*, from specimens preserved and stained. After Schaudinn [51], × about 2000. *a.fl*, anterior flagellum; *p.fl*, posterior flagellum; *r*, rostrum; *vac*, vacuole. (The flagella are not represented quite long enough.)

In *Coccidium lacazei* and *Adelea ovata* the formation of the microgametes differs in one important point from the process described above. When the nucleus of the microgametocyte breaks up, the karyosome divides up first, and its fragments travel to the periphery and act as centres round which the chromatin is concentrated to form the nuclei of the microgametes. Hence each microgamete possesses a karyosome. The microgametes of *C. lacazei* (Fig. 53, *c* and *f*) are smaller (3-4 $\mu$ in length) than those of *C. schubergi*, though otherwise similar, but those of *A. ovata* have no flagella, and move by undulations of the whole body.

The macrogametocytes are distinguished both from ordinary schizonts and from microgametocytes chiefly by two points (Fig. 51,

may be much less marked than is the case in *Coccidium schubergi*; compare especially the case of *Caryotropha mesnilii* (p. 223 and p. 225).

VI ♀). In the first place, they are more or less bean-shaped, and only become spherical during the maturation stages. In the second place, they are early marked out by the fact that from the youngest stages of the trophozoite onwards, they store up in their cytoplasm large quantities of reserve material in the form of the so-called plastinoid granules, bodies varying in diameter from $\frac{1}{2}\ \mu$ to $1\ \mu$, and very refringent, rendering the macrogametocytes whitish and opaque. The protoplasm is coarsely alveolar, and contains also another kind of granule less abundantly. The quantity of food-substance which the macrogametocytes store up retards their development considerably, so that they lag behind the male cells in this respect.

The plastinoid granules are very characteristic of Coccidia, and consist of a substance termed *Coccidin* by Labbé, which resembles, but is distinct from, the granules of paraglycogen, pyxinin, etc., found in Gregarines. The plastinoid granules are stained yellow by iodine (not wine-coloured, like the paraglycogen granules), and retain this colour after treatment with sulphuric acid; they are not soluble in weak acids or alkalis, nor in ether, chloroform, or alcohol. They are not stained by haematoxylin solutions, nor by Heidenhain's Iron-Alum method, nor yet by picrocarmine or borax-carmine; they are evenly stained, like the protoplasm, by Eosin, Aurantia, and Thionin; and Rhumbler's Eosin-Methyl Green mixture tinges them red. The other kind of granule mentioned above is distinguished by taking haematoxylin stains, especially by Heidenhain's method. (See Schaudinn [51], p. 250; Wasielewski [7], p. 51; and references.)

Each macrogametocyte becomes a single macrogamete, and to this end it goes through a process of maturation which has some points of resemblance to the development of the microgametes, but differs as widely as possible in detail (Fig. 51, VII ♀). The schizogony is completely suppressed, and maturation is effected simply by the expulsion of the karyosome, which travels during the space of about one hour from the centre to the periphery of the nucleus. It then passes out into the cytoplasm, and there breaks up at once with explosive rapidity into numerous small fragments which are expelled from the cell-body. During these events the macrogamete changes its bean-shaped form by slow contraction into a spherical one, the entire process lasting about two hours. Schaudinn suggests that it is the plastinoid granules which by their pressure during the changes of body-form squeeze out the fragments of the karyosome from the cytoplasm, as a cherry-stone can be squeezed out of a cherry. The contractions of the body have also the further effect of setting free the macrogamete from the shrivelled host-cell, so that it now lies free in the lumen of the gut of the host. The mature macrogamete is a spherical cell with a large spherical *pronucleus*, as it may now be termed, containing chromatin-granules but no karyosome. It is now ripe for fertilisation, and is attractive to the microgametes, many of which swarm round the macrogamete, but only one effects the actual fertilisation (Fig. 51, VIII ♀). At one spot the female pronucleus approaches the surface of the macrogamete, and here a "cone of reception" is formed as a little prominence of clear hyaline protoplasm, from which a thin streak of similar substance extends as far as the nucleus. A microgamete touches the cone and adheres to it. The cone of reception is at once drawn in, and partly in this way, partly by its own movements, the microgamete penetrates the macrogamete, and its pronucleus reaches the female pronucleus. No sooner is the entry of the microgamete completed than a clear membrane, gradually increasing in distinctness, appears over the whole surface of the zygote, excluding the less fortunate microgametes, which die off and break up (Fig. 51, IX). The clear membrane very soon becomes an exceedingly tough protective envelope, the *oöcyst* (*oöc*), within which, after fusion of the two pronuclei of the zygote, the sporogony runs its course. When the oöcyst is completely formed, the parasite is in a condition to abandon the shelter of the host and to brave the outer world. The further development can take place inside or outside the host, indifferently.

It is apparent that the process of conjugation in the Coccidia bears the greatest resemblance to the fertilisation by the sexual process in animals and plants. Schaudinn has observed some curious points of considerable interest in this process. Before the macrogamete has expelled the fragments of its karyosome from the cytoplasm, it is not attractive to the microgametes, but no sooner has it done so than they are drawn to it as by a magnet. The attraction, which is evidently exerted by the substance of the karyosome itself, acts very suddenly, and reaches from 48 $\mu$ to 130 $\mu$. If exerted near to developing microgametes, it stimulates them to great activity; even still imperfect microgametes then develop flagella, and in their struggles to free themselves from the microgametocyte they carry away lumps of protoplasm with them. The substance of the karyosome seems to be absorbed by the microgametes that swarm to it, and the remarkable fact was observed that the attractive power of the macrogamete was limited as regards the number of microgametes drawn to it, the usual number being about twelve or fourteen. When this number was made up, fresh microgametes approaching the macrogamete were no longer attracted. After the substance of the karyosome has dissolved up, a fresh attraction seems to be exerted by the female pronucleus, which travels to the surface.

The fusion of the two pronuclei in the zygote takes place in a very remarkable manner. The female pronucleus passes back to the centre of the zygote and becomes drawn out in the form of an elongated spindle, on which the chromatin granules are arranged in parallel rows running in a meridional direction (Fig. 51, IX). The male pronucleus, at first huddled up at one pole of this nuclear spindle, also breaks up into granules of chromatin, which mingle with those of the female pronucleus, and cause the spindle to increase in size until it finally stretches through the entire oöcyst (Fig. 51, X). One pole of the spindle marks the point of entry of the microgamete, where its disappointed companions are still to be seen outside the oöcyst. The peculiar spindle-like arrangement of the nucleus in the zygote has nothing to do with nuclear division, but is simply a means of mixing intimately the chromatin derived from two different sources, and when this is effected the spindle contracts and rounds itself off, the final result being a spherical nucleus, the fusion-product of the two pronuclei. It is usually in the stage with the fertilisation-spindle that the oöcyst passes out of the body of the host.

The nucleus of the zygote proceeds to divide *by the direct method* (Fig. 51, XI, XII), first into two, then into four nuclei, round each of which the protoplasm segments into four masses, the *sporoblasts* (*archispores*, Labbé). A certain amount of granular protoplasm is left over as a cystal residuum, which occupies the centre of the cyst between the four sporoblasts, and is slowly absorbed during the further development. Each sporoblast acquires an oval form, the nucleus being at the centre (Figg. 51, XIII, and 54, *a*). On either side of the nucleus there is a clear spherical vacuole, one of eight similar vacuoles formed in the zygote containing a viscid substance derived, apparently, from the plastinoid granules before the sporoblasts were segmented off. The sporocyst is now secreted round the sporoblast in two coats; the gelatinous *epispore* appears first, then internal to it the tough refringent *endospore*. The sporoblast has now become the *spore*. As soon as the sporocyst is complete, the nucleus of the spore divides, again by the direct method (Fig. 54, *b* and *c*). The two daughter nuclei place themselves at the two opposite poles of the spore, while the two clear spheres come together at the centre and fuse into an oval body (Fig. 54, *d*). The protoplasm of the spore now segments into two sporozoites, each with a nucleus, and a central mass of residuary protoplasm containing the above-mentioned oval body, and also a number of plastinoid granules ejected from the sporozoites, which have coarsely alveolar protoplasm free from large granules (Figg. 51, XIV, and 54, *e*).

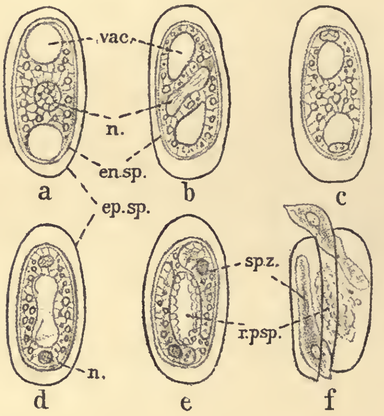

Fig. 54.

Development of the spore of *Coccidium schubergi*, Schaud. After Schaudinn [51], × 1500. *a*, sporoblast with spore-membranes, single nucleus, and two vacuoles. *b*, the nucleus is dividing. *c*, two nuclei placed at the two poles of the sporoblast, externally to the vacuoles. *d*, the vacuoles fusing together. *e*, two sporozoites, arranged *tête-bêche*, and a residual mass of protoplasm containing the vacuole. *f*, the sporocysts splitting and the two sporozoites escaping. *n*, nucleus; *vac*, vacuole; *en.sp*, endospore; *ep.sp*, epispore; *sp.z*, sporozoite; *r.p.sp*, residual protoplasm of the spore.

With the formation of the sporozoites the life-cycle has been brought back to its starting-point, and requires only the infection of a new host.

The sporogony takes two or three days in *Coccidium schubergi;* in *C. falciforme* of the mouse it takes as long as four days. The clear spheres mentioned above in the sporoblasts and spores can be isolated by crushing the spore, and are viscid, plastic bodies which dissolve in dilute or strong acids, and which, when treated with weak acetic or hydrochloric acid, swell up before dissolving—a property which Schaudinn believes to be largely instrumental in the bursting of the spore-envelope in the gut of a new host. The first effect of the digestive juices is to produce an aperture in the wall of the oöcyst (Fig. 51, XV). Then the sporocysts burst with a distinct jerk, always along an even meridional line, which, if preformed, cannot be detected beforehand. The sporozoites lie *tête-bêche* within the spore, and creep out in different directions (Fig. 54, *f*). The oöcysts, sporocysts, and residuary bodies are left behind and cast out with the faeces.

The infection of the *Lithobius* is always a casual one, by way of the digestive tract. Sometimes a centipede becomes infected by eating another of its kind; infection then is conveyed not only by the oöcysts, but by all other stages except the immature, not fully-grown schizonts or gametocytes, which pass out with the faeces after digestion of their host-cells. Frequently the faeces of infected centipedes are eaten by wood-lice (*Oniscus* and *Porcellio*). The contained oöcysts then pass through the gut of the wood-louse quite unaltered; but if a wood-louse containing an oöcyst be eaten by a centipede, the latter will become infected. In this case the wood-louse is not an intermediate host, but a simple carrier.

It follows from the mode of infection that centipedes living in a confined and restricted area have a much greater chance of taking the infection from one another, and Schaudinn found that a very large proportion of the specimens of *Lithobius* obtained by him from outhouses in the grounds of the Zoological Institute at Berlin were infected with the parasites, but that *Lithobii* collected in the woods and forests were generally free from them.

In moles infected by *Cyclospora*, Schaudinn [51*a*] found that the infection was not transmitted by cannibalism, although these pugnacious animals frequently eat each other. He believes that in nature the mole becomes infected by eating wood-lice and other dung-feeding Arthropods, which have fed on the faeces of other infected moles.

The variations in the morphology and development of other Coccidia, as compared with the type here selected, are best considered under two heads: first, structural and morphological variations in the individual stages of the life-history; secondly, variations in the composition of the life-cycle considered as a whole.

(1) *Morphology.*—Some of the differences between *Coccidium schubergi* and its two colleagues, *C. lacazei* and *Adelea ovata*, have

already been noticed incidentally, but a few other points require special mention in other forms.

The schizogony is usually very similar in its characters to that described above, and always lacks cyst-membranes of any kind, whether round the schizont as a whole or in the form of spore-envelopes. The term "Eimerian cyst," so frequently employed, is therefore a misnomer. There is always a large amount of residuary protoplasm, and when the formation of the merozoites is completed, they very frequently take on a characteristic arrangement, like that of the divisions of an orange or the staves of a barrel; hence this stage is termed by French writers the "corps en barillet"; it is homologous with the "stade en rosace" of the

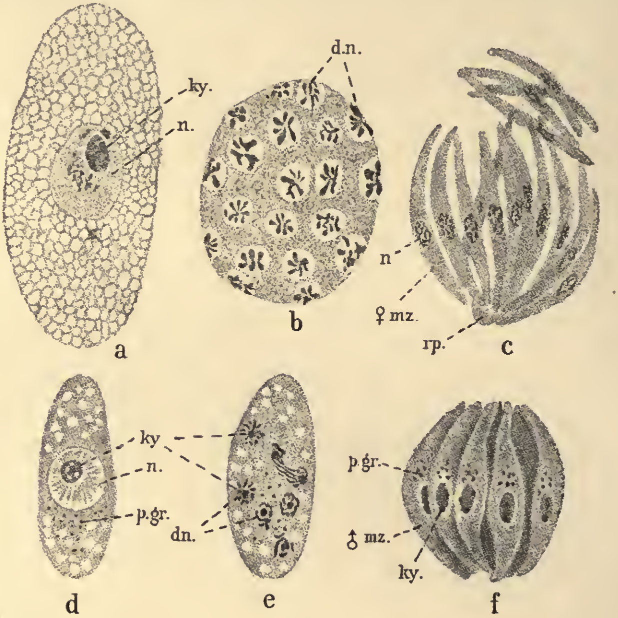

Fig. 55.

Schizogony of *Adelea ovata*, A. Schn. (par *Lithobius forficatus*), after Siedlecki [55]. *a-c*, ♀ generation; *d-f*, ♂ generation. *a*, full-grown ♀ schizont (*macroschizont*), with a large nucleus (*n*) containing a conspicuous karyosome (*ky*). *b*, commencement of schizogony; the nucleus has divided up to form a number of daughter nuclei (*d.n*), each consisting of a number of rods of chromatin arranged in a star-shaped manner in a clear space. The karyosome of stage *a* has broken up into a great number of daughter karyosomes, each of which forms at first the centre of one of the star-shaped daughter nuclei; but in a short time the daughter karyosomes become inconspicuous, and seem to be absorbed, or to be got rid of in some way. *c*, completion of schizogony; the ♀ schizont has broken up into a number of *macromerozoites* (♀ *mz*), implanted on a small quantity of residual protoplasm (*r.p*). Each ♀ merozoite has a chromatic nucleus (*n*) without a karyosome. *d*, full-grown ♂ schizont (*microschizont*), with nucleus (*n*), karyosome (*ky*), and a number of characteristic pigment-granules (*p.gr*). *e*, commencement of schizogony. The nucleus is dividing up into a number of daughter nuclei (*d.n*), each with a conspicuous karyosome (*ky*). *f*, completion of schizogony. The numerous micromerozoites (♂ *mz*) have each a nucleus with a conspicuous karyosome (*ky*) at one pole, and the protoplasm contains pigment-granules (*p.gr*) near the nucleus, on the side furthest from the karyosome.

Haemosporidia. When the merozoites are very numerous they may be disposed in a double series. The remarkable form parasitic on *Polymnia*, recently described by Siedlecki [55*a*] under the name *Caryotropha mesnilii*, presents an interesting divergence from the usual type of schizogony. The schizont divides first into ten or fifteen large rounded cells, termed by Siedlecki *schizontocytes* (Fig. 67). Each schizontocyte then gives origin to twenty or thirty merozoites, so that the host-cell finally contains not one but many "barillets" (Fig. 67, *d*). This method of schizogony recalls the formation of spores in *Porospora* (see above, p. 188), and is also interesting for its relation to the formation of the gametes (p. 225).

In *Coccidium schubergi* and most other Coccidia the schizonts show no trace whatever of sexual differentiation until the final term of the schizogony, when they become gametocytes of two kinds, distinct from one another and from the ordinary schizonts. A most important variation of this type is seen in *Adelea ovata* (Fig. 55) and some other species, where the trophozoites formed from the sporozoites exhibit sexual characters from the outset, and can be distinguished as male or female, but multiply asexually through many schizogonous generations before finally giving rise to gametes. An extreme case of sexual differentiation during schizogony is seen, according to Schaudinn [51*a*], in *Cyclospora caryolytica* from the mole, where no differentiation can be observed in the sporozoites themselves, but is discernible in the trophozoites produced from them after one hour's growth. The female schizonts of *Cyclospora* have coarsely alveolar cytoplasm of very fluid consistence, and without any reserve substances. The male schizonts are characterised by the possession of strongly refractile, pigment-like granules. The merozoites produced from the two classes of schizonts also differ markedly both in character and arrangement. The female gametocytes have a coarsely alveolar cytoplasm packed with large granules of reserve material resembling yolk, while the male gametocytes are distinguished by cytoplasm which is extremely finely granulated and stains very readily. In this species, therefore, four distinct classes of trophozoites can be distinguished.

In some Coccidia—for example, *Adelea ovata*, *A. mesnili*, *Eimeria nova*, and *Klossia helicina*—the number of microgametes produced from a microgametocyte is not indefinite, but constantly four only. This reduction in the number of microgametes is usually correlated with a precocious association of the gametocytes, a condition resembling that which is commonly seen in Gregarines. Thus in *A. ovata* the macrogametocytes when full-grown fall out of their host-cells and pair with microgametocytes, which may be not full-sized. The two cells adhere together, and the female cell undergoes maturative changes, becoming a macrogamete, while the microgametocyte produces four microgametes (Fig. 56). One of the latter fertilises the ripe macrogamete, while the other three perish.

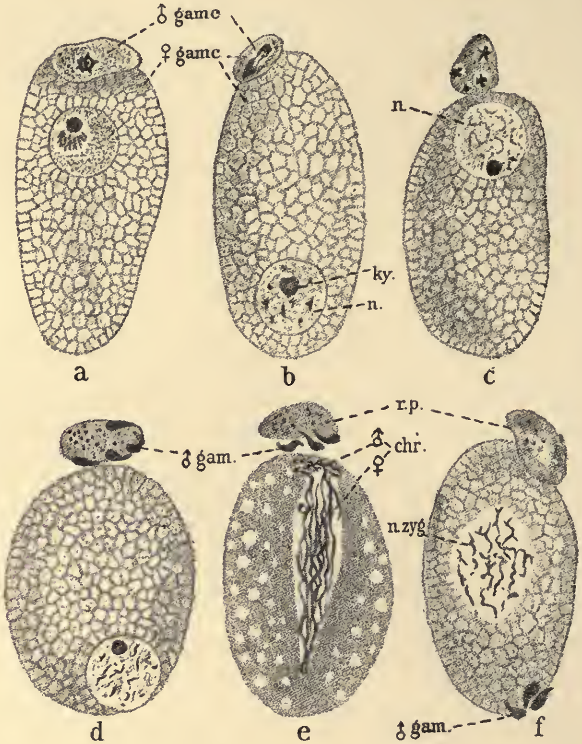

Fig. 56.

Conjugation of *Adelea ovata*, A. Schn. (par. *Lithobius forficatus*), after Siedlecki [55], slightly modified. *a*, a microschizont, not full-grown (compare Fig. 55, *d*), becomes a microgametocyte (♂ *gamc*) and attaches itself to a macroschizont or macrogametocyte (♀ *gamc*). *b*, the nucleus of the microgametocyte divides—*c*, into four daughter nuclei, which become—*d*, four microgamtes (♂ *gam*). The karyosome of the microgametocyte disappeared when division of the nucleus commenced. *e*, one of the microgametes penetrates the macrogamete, which forms a fertilisation-spindle, composed of ♂ and ♀ chromatin (*chr*), still distinct from each other, and occupying opposite poles of the spindle. The other three microgametes (♂ *gam*), and the residual protoplasm of the microgametocyte (*r.p*), containing the pigment granules, perish and disintegrate on the outside of the macrogamete. The karyosome of the macrogamete has broken up, and disappeared as such. *f*, the complete union of the chromatin from the two sources produces the single nucleus of the zygote (*n.zyg*).

*Note.*—In this conjugation an apparent difference in the stages is caused by the position of the nucleus of the ♀ gamete, which places itself at one pole of the body, either at the pole nearest to the microgametocyte (*a*, *c*, *e*) or at the pole furthest from it (*b*, *d*, *f*). In the first case the fertilising microgamete penetrates the microgamete at once, and the three residuary microgametes are formed near the remains of the microgametocyte. In the second case all four microgametes travel round to the pole furthest from the microgametocyte, where penetration of the fertilising element takes place (*f*).

In *A. mesnili* and *Eimeria nova* the development is similar, but the gametocytes may or may not associate before the maturity of the macrogamete. In *Klossia helicina* precocious association of the gametocytes occurs, but in this case the female parasite is not set free from the host-cell. Several microgametocytes penetrate into a kidney-cell containing a macrogametocyte, and there form each four microgametes, one of which fertilises the macrogamete when mature. In all these cases the economy effected in the number of microgametes produced is probably related to the early pairing of the gametocytes, and the consequent certainty that the union of the gametes will be effected.

In the formation and maturation of the gametes, the most essential feature in the instance selected is the elimination in both sexes of the karyosome, which, like the macronucleus of Infusoria, would appear to represent effete nuclear substance which is cast out and formed anew at conjugation. The karyosome is not, however, always eliminated *before* the actual union of the gametes. To go no further than the *Lithobius*, in *Coccidium lacazei* and *Adelea ovata* the karyosomes are retained in both the gametes, and the same is the case in *Coccidium proprium*, A. Schn., of *Triton*. In all these instances, however, the karyosomes are left behind in the residual protoplasm of the oöcyst, and do not pass on into spores or sporozoites, so that the result is the same. In *Coccidium lacazei*, correlated with this difference, Schaudinn observed microgametes swarming round immature, half-grown macrogametes, which they never do in *C. schubergi*.

In *Cyclospora caryolytica* the karyosome of the male gametocyte becomes divided each time that the nucleus divides, and the nucleus of each microgamete contains, at first, a distinct karyosome; but as the nucleus assumes its definitive, elongated form, the karyosome is suddenly ejected from it, and is left behind by the microgamete when it swims off. In the macrogametocyte of this species a very interesting process of maturation takes place. The karyosome first becomes fragmented to form a clump of fine granules, constituting a chromatic nucleus, which divides by a primitive form of karyokinesis into two. One of the two daughter nuclei divides again in a similar manner. Three nuclei are thus formed, two of which become slowly absorbed in the cytoplasm, and represent as it were polar bodies cast off in order to bring about a process of nuclear reduction. The third remaining nucleus becomes the pronucleus of the macrogamete (see also below, p. 273).

In *Adelea ovata*, according to Siedlecki, the two consecutive nuclear divisions to form the four microgametes are different from one another: the first is regular and resembles karyokinesis, the second simply divides the chromatin into two halves. The author believes that the first division reduces the quantity of chromatin, the second the number of chromosomes. In this form also a quantity of chromatin is eliminated from the macrogametocyte at maturation, prior to fertilisation. The maturation of *Adelea ovata* would thus seem to approach more nearly the Metazoan type than does that of *Coccidium schubergi*.

In *Caryotropha* the microgametocyte does not divide up at once into microgametes, but first into a number of spherical cells, which may be termed microgametocytes of the second order, and each of which gives rise to numerous microgametes. Hence in this form the correspondence between the ordinary schizogony and the formation of the microgametes is very exact (see above, p. 223).

The microgametes vary greatly in their characters. Only 3-4 μ long in *Coccidium lacazei*, they reach ten times that length in *Klossia*, but in each case are scarcely 1 μ in breadth. The flagella were first discovered by Léger in the microgametes of *Barroussia caudata*, Léger, from *Lithobius martini*, and in other forms. They have now been demonstrated in a number of species; and though usually two in number, they may vary in position; in the above species of *Barroussia* and in *Coccidium oviforme* of the rabbit, both flagella are attached to the anterior end of the gamete.

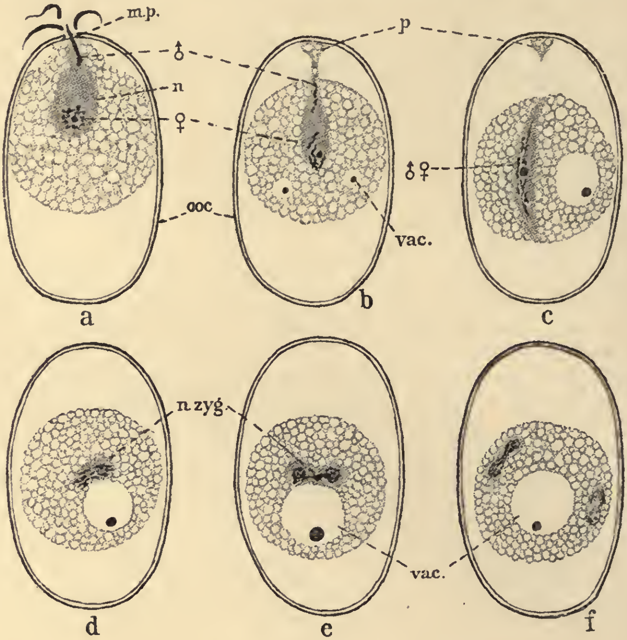

Fig. 57.

Conjugation of *Coccidium proprium*, A. Schn. (par. *Triton*), after Siedlecki [53]. *a*, penetration of a microgamete (♂) through the micropyle (*mp*) of the tough oöcyst (*oöc*), by which the female gamete is surrounded. The ♀ gamete only partially fills the oöcyst, which it only touches at the micropyle. Its nucleus (*n*) has lost its membrane, and is pear-shaped, with ill-defined limits; it touches the micropyle by one of its extremities, and at the opposite extremity the chromatin (♀) is aggregated in the form of a number of little rods round a central karyosome. *b*, the microgamete after penetration breaks up into a mass of chromatin (♂). The macrogamete has withdrawn from the micropyle, leaving a plug of protoplasm (*p*) attached to it, which closes the aperture. Two vacuoles (*vac*) have appeared in the macrogamete, containing each a little chromatic sphere, perhaps derived from the karyosome. *c*, a fertilisation-spindle is formed, in which the ♂ and ♀ chromatin granules are commingled. The two vacuoles have fused into a single one, which persists throughout the sporulation, and is left in the residuary protoplasm of the cyst. *d*, *e*, *f*, the nucleus of the zygote (*n.zyg*) becomes compact (*d*), then divides into two nuclei (*e*, *f*), and finally into four.

Finally, in *Adelea ovata*, as already mentioned, and in *Benedenia eberthi* (Fig. 58, *c*), the flagella are totally absent, and the microgamete moves by undulating movements of the whole body.

Two interesting variations are seen in the condition of the macrogamete at fertilisation, which add to the striking resemblance between this process in Coccidia and the fertilisation of the ovum in Metazoa. In *Coccidium schubergi* and many others the macrogamete is naked until the penetration of a microgamete into its substance has been effected, whereupon the oöcyst at once commences to be secreted, barring out other microgametes. But in *C. proprium*, parasitic in newts (Fig. 57), the oöcyst is secreted round the macrogamete before fertilisation ; within the tough membrane the protoplasm contracts and is in contact with it only at one point, where a micropyle is formed, a minute pore through which the microgamete enters (Fig. 57, *a*). When this event has taken place the micropyle is closed up and the protoplasm withdraws from it (Fig. 57, *b* and *c*). A fertilisation-spindle occurs in this species, similar to that described above, but apparently less regular in arrangement. Since in *Coccidium oviforme* of the rabbit the protoplasm of the macrogamete is also contracted and does not fill the oöcyst (see Fig. 62), it is not improbable that the envelope in question is formed before fertilisation as in *C. proprium*.

In *Cyclospora caryolytica* the fertilisation is remarkable for the occurrence of polyspermy (Schaudinn [51*a*]). A great number of microgametes enter the macrogamete, but only one fuses with the female pronucleus, the others being absorbed in the cytoplasm. In other respects the fertilisation is of the usual type, with formation of a fertilisation-spindle and secretion of a tough oöcyst round the zygote.

In the sporogony the greatest variation occurs, and as the modern classifications of the Coccidia are founded entirely upon the character of the spores and their formation in the different types, it is sufficient to refer to the systematic review below for information on these points. It may be noted, however, that the spores of Coccidia are usually of simple form, the sporocysts not prolonged into the tails, spines, or other processes so common in Gregarines and in Myxosporidia, the only exceptions to this rule being *Minchinia chitonis* (Fig. 66, *a*), *Echinospora labbei* (Fig. 66, *c*), and *Barroussia caudata ;* and further, that with very few exceptions the number of sporozoites present in the Coccidian spore does not exceed four, and seems never to be eight, the usual number in Gregarines.

(2) *Variations in the Life-Cycle.*—Although there are but few Coccidia, relatively, in which the life-cycle has been studied in full detail, yet some important differences have already been made known between the different species so far investigated. It has already been stated above that *Adelea ovata* differs from its two colleagues in *Lithobius* in the important fact that the sporozoites which start the life-cycle in a new host give rise from the first to sexually differentiated schizonts, which proceed to multiply by schizogony for a number of generations before finally giving rise to the gametes.

In *Benedenia eberthi* from *Sepia*, the sporozoites give rise to indifferent trophozoites, which, however, when full-grown, become gametocytes, which give rise at once to gametes, so that in this form *the schizogonous cycle does not exist.*

The life-cycle of *Benedenia* is therefore of a simple type, and

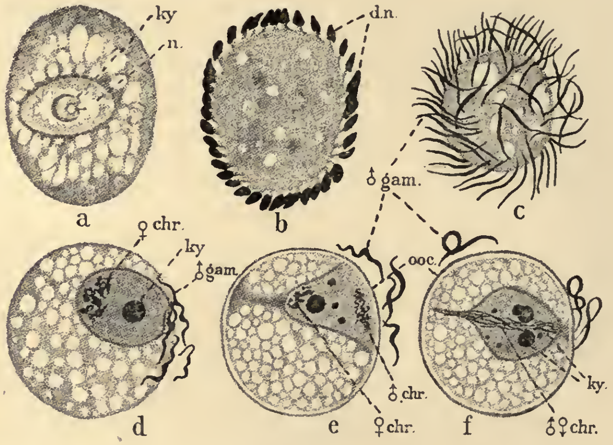

FIG. 58.

Formation of gametes and conjugation, in *Benedenia eberthi*, Labbé (par. *Sepia*), ×600, after Siedlecki [52]. *a*, adult undifferentiated trophozoite, capable of giving rise to microgametes, or of becoming a macrogamete. *n*, nucleus; *ky*, karyosome. *b* and *c*, formation of microgametes. *b*, the nucleus of the gametocyte has divided into numerous daughter nuclei (*d.n*), which travel to the periphery and project from the protoplasmic body. *c*, each daughter nucleus becomes an elongated vermiform microgamete (♂ *gam*), composed principally of chromatin, with a small quantity of protoplasm. *d, e, f*, conjugation. *d*, in the macrogamete the nucleus places itself in contact with the surface of the body, and by condensation of the chromatic network a mass of chromatin (♀ *chr*) is formed at the pole of the nucleus furthest from the surface of the body. *ky*, karyosome; ♂ *gam*, microgametes swarming round the macrogamete in the vicinity of the nucleus. *e*, a microgamete has penetrated the macrogamete, and is broken up to form a mass of chromatin-granules (♂ *chr*). A membrane, the oöcyst (*oöc*), is now formed round the zygote, excluding the other microgametes. *f*, a fertilisation-spindle is formed, in which the chromatin-granules derived from the two gametes (♂ and ♀ *chr*) is commingled.

only differs from that commonly seen in Gregarines in certain details of the conjugation. Its entire history may be expressed as follows :—

$$\left.\begin{array}{l}\text{Sporozoite}\rightarrow\text{♂ Gametocyte}\times n\text{ ♂ Gametes}\\ \text{Sporozoite}\rightarrow\text{♀ Gametocyte}\rightarrow\text{♀ Gamete}\end{array}\right\}+=\text{Zygote (Oöcyst)}\times m\text{ Spores}\times mn\text{ Sporozoites.}\quad[n=3.]$$

The life-cycle of *Adelea ovata* is similar, but the complication of schizogony is introduced :—

$$\begin{array}{l}\text{Sporozoite}\rightarrow\text{♂ Gametocyte (Microschizont)}\times\text{♂ Merozoites (Micromerozoites)}\rightarrow\ldots\\ \text{Sporozoite}\rightarrow\text{♀ Gametocyte (Macroschizont)}\times\text{♀ Merozoites (Macromerozoites)}\rightarrow\ldots\end{array}$$

$$\left.\begin{array}{l}\rightarrow\text{♂ Gametocyte}\times 4\text{ ♂ Gametes}\\ \rightarrow\text{♀ Gametocyte}\rightarrow\text{♀ Gamete}\end{array}\right\}+=\text{Zygote (Oöcyst)}\times m\text{ Spores}\times mn\text{ Sporozoites.}\quad[n=2.]$$

Finally, in *Coccidium schubergi* and other forms the fullest complication is developed :—

$$\begin{array}{l}\text{Sporozoite}\rightarrow\text{Schizont}\times\text{Merozoites}\rightarrow\ldots\text{ Schizonts}\times\text{Merozoites}\rightarrow\\ \text{Sporozoite}\rightarrow\text{Schizont}\times\text{Merozoites}\rightarrow\ldots\text{ Schizonts}\times\text{Merozoites}\rightarrow\end{array}$$

$$\left.\begin{array}{l}\text{♂ Gametocytes}\times n\text{ ♂ Gametes}\\ \text{♀ Gametocytes}\rightarrow\text{♀ Gametes}\end{array}\right\}+=\text{Zygote}\times m\text{ Spores}\times mn\text{ Sporozoites}\quad[m=4,\ n=2.]$$

It is thus seen that the life-cycles of the Coccidia can be arranged in what is evidently a natural series; but it is open to debate which end of the series should be considered as the more primitive, and should be taken as the starting-point of the evolution. The tendency of modern authorities has been rather to consider the condition in *Coccidium* as primitive, and to regard *Benedenia* as a form in which the alternation of generations is secondarily suppressed. It does not, however, seem probable that a method of reproduction so useful to the parasite as the schizogony would have been abandoned when once acquired, and the existence of the vast legion of Gregarines, in which schizogony is of the rarest occurrence, makes it probable that in Coccidia also the primitive ancestral type was without schizogony, and that the alternation of generations has been acquired by the majority of the group as an adaptation to parasitic life. But even assuming the correctness of this view, it does not necessarily follow that the case of *Benedenia* itself is primitive. More intimate acquaintance with the life-cycles of different Coccidia is necessary before a definite opinion can be framed with regard to this point.

(*c*) *Classification.*—The order Coccidiidea is divided into families characterised by the number of sporocysts (if any) formed within the oöcyst. Generic characters are sought chiefly in the number of sporozoites formed in each spore, and to a less extent in the form and characters of the sporocyst. Four families are thus recognised, but the differences which separate the first of them, the *Asporocystidae*, from the other three are such as should give it the rank of a sub-order rather than a family.[1]

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[1] The classification of Labbé [4] is founded upon the number of uninucleate masses or *archispores* into which the schizont or sporont divides up in the first instance. In *Eimeria* each archispore becomes a sporozoite; in other forms each archispore becomes a sporoblast which secretes the sporocyst, and then may further divide up to form sporozoites. On this basis of division Labbé founds two sub-orders —I. Polyplastina, with numerous archispores (*Eimeria*, *Klossia*, *Adelea*, etc.); II. Oligoplastina, with few (2-4) archispores (*Coccidium*, *Diplospora*, etc.).

Léger [47] considers that the primary subdivision of the Coccidia should be based upon the number of sporozoites formed in each oöcyst. He therefore classifies them as follows:—

A. Coccidia with polyzoic oöcysts, including (1) *Asporocystidae* (*Eimeria*), with no sporocysts; and (2) *Polysporocystidae*, with sporocysts, which are monozoic (*Barroussia*), dizoic (*Adelea*), trizoic (*Benedenia*), or tetrazoic (*Klossia*).

B. Coccidia with octozoic oöcysts, including (1) *Disporocystidae*, with two tetrazoic sporocysts (*Diplospora*); and (2) *Tetrasporocystidae*, with four dizoic sporocysts (*Coccidium*, *Crystallospora*).

C. Coccidia with tetrazoic oöcysts, including one genus (and family ?) *Cyclospora*, with two dizoic sporocysts.

Mesnil [49], on the other hand, divides the Coccidia into two divisions, the Asporocystea and the Sporocystea. The Asporocystea are to include the Asporoblastea *seu* Monosporoblastea, for the species *Legerella* (*Eimeria*) *nova*, and the Sporoblastea, for the malarial parasites. The Sporocystea are the ordinary Coccidia.

It should be noted that the four families of Coccidia now generally recognised are not named in accordance with the accepted rules of zoological nomenclature, which require that a family should be named from its type-genus. Thus the *Asporocystidae*

Family 1. Asporocystidae, Léger (Tribe *Monosporea*, A. Schneider). No sporocysts are formed within the oöcyst; the sporozoites are naked (gymnospores).

Genus 1. *Eimeria*, A. Schn., 1875 (*Legerella*, Mesnil, 1900). With the characters of the family.

The genus *Eimeria* was founded by Aimé Schneider for the *Gregarina falciformis* described by Eimer (1870) from the intestine of the mouse. The diagnostic generic character was the absence of sporocysts. Several other species were afterwards added by Schneider and others to the genus. The rapid advances that have been made within recent years in our knowledge of the life-histories of Coccidia have shown that nearly all the species of *Eimeria* are nothing but the schizogonous generations of Coccidia belonging to other genera and species. Thus the type species, *E. falciformis* of the mouse, becomes *Coccidium falciforme; E. schneideri*, Bütschli, from *Lithobius*, is the schizont of *Adelea ovata;* while *E. schneideri*, Schneider *non* Bütschli, appears to be that of *Coccidium lacazei* (Labbé). *E. nepae* is probably identical in like manner with *Barroussia ornata* from the same host. In the light of these facts, it appeared, until recently, extremely probable that the name *Eimeria* was about to become a *nomen nudum*, a fate which has already overtaken the "Eimerian" genera *Pfeifferia* seu *Pfeifferella*, Labbé; *Karyophagus*, Steinhaus; *Cytophagus*, Steinhaus; *Acystis*, Labbé (founded to include the two foregoing); *Gonobia*, Mingazzini; *Molybdis*, Pachinger; and *Cretya*, Mingazzini.

Quite recently, however, it has been discovered by Léger [47] and Bonnet-Eymard [31] that one species, at least, of *Eimeria* has claims to independent recognition. *E. nova*, A. Schn., from the Malpighian tubules of *Glomeris* has been thought to be the Eimerian stage of *Cyclospora glomericola*, A. Schn., from the same host; but *Glomeris guttata* in Provence, and *G. ornata* in the Dauphiné, are infected with the *Eimeria*, but not with the *Cyclospora*. Examination of the *Eimeria* shows further that it has a typical alternation of generations; schizogony, with differentiated male and female schizonts, as in *Adelea ovata*, is followed by sporogony, with the formation of a zygote which breaks up within a resistent oöcyst into thirty or forty naked sporozoites, arranged side by side, or in a twisted bundle.

*Eimeria nova* remains, therefore, an independent species, the only one[1] at present contained in the genus after subtraction of those which are merely schizonts of other species. The true *Eimeria* is easily distinguished from the false by the fact that its naked sporozoites are enclosed in a resistent oöcyst, whereas in schizogony there is no cyst-envelope of any sort enclosing the merozoites.

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should be *Eimeridae* (or *Legerellidae*); the *Disporocystidae* should be *Isosporidae;* the *Tetrasporocystidae* should be *Coccididae* (or *Eimeridae*); and the *Polysporocystidae* should be *Klossidae*.

[1] Since this was written Cuénot [32] has described another species of *Eimeria*, under the name *Legerella testiculi*, which is parasitic in the testis of *Glomeris marginata*, and therefore occurs only in one sex of the host. In this form precocious association occurs between a macrogametocyte and one or two microgametocytes, as in *Adelea ovata*.

Mesnil has proposed, however, the new generic name *Legerella* for *Eimeria nova*, on the ground that the use of the name *Eimeria* is inconvenient now that all the other species have been found to be simply schizogonous stages. Experts learned in the laws of zoological nomenclature may decide how far such a course is justifiable and proper.[1]

FAMILY 2. DISPOROCYSTIDAE, Léger (Tribe *Disporea*, A. Schneider). The oöcyst contains two spores (chlamydospores).

Genus 2. *Cyclospora*, A. Schn., 1881. Spores dizoic.

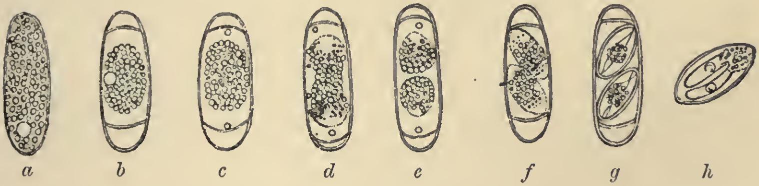

FIG. 59.

Sporogony of *Cyclospora glomericola*, A. Schn. (par. *Glomeris*). *a*, oöcyst freshly encysted. *b*, the contents of the oöcyst have contracted, and a partition is formed at each end. *c*, *d*, *e*, formation of the two sporoblasts. *f*, the sporoblasts developing into spores. *g*, oöcyst with ripe spores. *h*, spore more highly magnified, showing the two sporozoites and the sporal residuum. From Wasielewski, after A. Schneider.

The type-species is *C. glomericola*, A. Schn., from the intestinal epithelium of *Glomeris*. Very recently Schaudinn [51*a*] has described in great detail the life-cycle of another species, *C. caryolytica*, Schaud., which occurs as an intranuclear parasite of the intestinal epithelium of the mole.

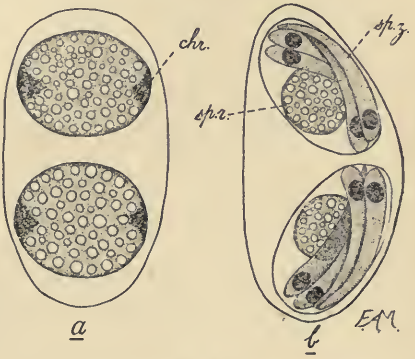

FIG. 60.

Cysts of *Diplospora lieberkühni* (Labbé), (par. *Rana esculenta*). *a*, cyst with two sporoblasts, each with two chromatin masses (*chr*). *b*, cyst with two ripe spores, each containing four sporozoites (*sp.z*) and a sporal residuum (*sp.r*). After Laveran and Mesnil [40], × 1000.

Genus 3. *Diplospora*, Labbé, 1893. Spores tetrazoic.

Type-species, *D. lacazei*, Labbé (including *D. rivoltae*, Labbé), from a great number of birds. Others are *D. cammillerii*, Hagenm., from the lizard *Gongylus ocellatus*; *D. mesnili*, Sergent [51*b*] from *Chamaeleo vulgaris*; and *D. laverani*, Hagenm., from the snake *Coelopeltis lacertina*, both occurring in Algeria. *D. lieberkühni* (Labbé) (Fig. 60), occurring in the kidneys of *Rana esculenta* (where it was first noted by Lieberkühn in 1854), has been made by Labbé the type of his genus *Hyaloklossia*

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[1] Stiles [59] has recently proposed the name *Eimeriella*, as a substitute for *Eimeria*, on the ground that the latter name belongs, by right of priority, to the genus commonly known as *Coccidium* (see below, p. 232, footnote).

(*vide infra*, p. 236). The reproduction of *D. lacazei* has been studied by Laveran. By many authors this genus is united with the following.[1]

Genus 4. *Isospora*, A. Schn., 1881. Spores polyzoic.

*I. rara*, A. Schn., from the black slug *Limax cinereo-niger* (kidneys ?), characterised by having numerous sporozoites in each spore (Fig. 61).

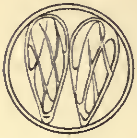

FIG. 61.

Oöcyst of *Isospora rara*, A. Schn. (par. *Limax* sp.), showing the two polyzoic spores. From Wasielewski, after A. Schneider.

FAMILY 3. TETRASPOROCYSTIDAE, Léger (Tribe *Tetrasporea*, A. Schn.). The oöcyst contains four spores (chlamydospores).

Genus 5. *Coccidium*, Leuckart, 1879. The dizoic spores are spherical or oval.

A very large number of species, confined, with few exceptions (see p. 206), to Vertebrate hosts, and occurring commonly in all kinds of Vertebrates. The type and best-known species is the common *C. oviforme*, Leuck.,[2] from the rabbit (Figs. 47 and 62), which is said to be found occasionally also in man (see reference on p. 209). In Sauropsida the prevailing type is *Diplospora* (see above), but

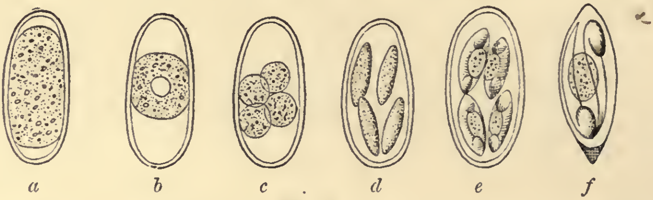

FIG. 62.

Spore formation in *Coccidium oviforme*, Leuck., from the liver of the rabbit. After Balbiani, from Wasielewski. *a*, encysted individual (zygote) in which the protoplasm is beginning to shrink away from the oval oöcyst at the two poles. *b*, the zygote has contracted itself into a spherical form. *c*, segmentation into four sporoblasts. *d*, elongation of the sporoblasts to form spores. *e*, four complete spores in the oöcyst. *f*, single spore more highly magnified, showing the two sporozoites and a small quantity of residual protoplasm.

*Coccidium raillieti*, Léger, has been described from the intestine of the slow-worm *Anguis fragilis* ; and *C. delagei*, Labbé, from that of the water-tortoise *Cistudo europaea* ; while *C. tenellum*, Railliet, with several varieties, is found in birds. In mammals and in Ichthyopsida numerous species are found.

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[1] Laveran, Mesnil, Schaudinn, and Blanchard are apparently of opinion that Schneider's description of *Isospora rara* as polyzoic was erroneous, and regard this species as tetrazoic, thereby making the genera *Isospora* and *Diplospora* synonymous. Hence, since *Isospora* is the older name, they make use of it for all the species here termed *Diplospora*. But until Schneider's type of *Isospora* has been re-examined, it is somewhat premature to *assume* that so experienced and distinguished an investigator was in error in describing it as polyzoic.

[2] But according to Labbé [4] the name *Psorospermium cuniculi*, Rivolta, 1878, is prior to *Coccidium oviforme*, Leuckart, 1879 ; the correct designation of the species would therefore be *Coccidium cuniculi* (Rivolta). According to Stiles [58], on the other hand, the species was named *Monocystis stiedae* by Lindemann in 1865. Since, moreover, the type-species of *Eimeria* (*E. falciformis*) has proved to be a *Coccidium*, this author claims that *Eimeria* 1875, as a generic name, has priority over *Coccidium* 1879. The conclusion is that *Coccidium* as a generic name should disappear, and the Coccidian parasite of the rabbit's liver should be called *Eimeria stiedae* (Lindemann). Lühe (48*a*) is of the same opinion as regards the application and validity of the generic names *Eimeria* and *Coccidium*.

Laveran and Mesnil [59] have recently described a species from the intestine of the frog (*Rana esculenta*), in which the sporocysts, after being formed in the usual manner, become redissolved, leaving the eight sporozoites free in the cyst, thus bringing about secondarily a condition similar to that which characterises the genus *Eimeria*. The authors consider this form sufficiently distinct to be the type of a new subgenus, and name it *Paracoccidium prevoti* (Fig. 63). Still more recently [40] these authors have described a species of *Coccidium* from the rectum of the tortoise *Damonia reevesii*, under the name of *C. mitrarium*, which is remarkable for having oöcysts shaped like a mitre, and is also unique amongst Coccidia in being an extracellular parasite.

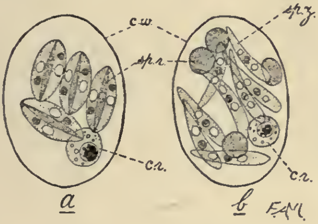

FIG. 63.

Cysts of *Paracoccidium prevoti*, Lav. et Mesn. (par. *Rana esculenta*). *a*, cyst with four spores and a cystal residuum (*c.r*). Each spore contains two sporozoites and a sporal residuum (*sp.r*). *b*, ripe cyst in which the sporocysts have become dissolved, setting free their contents; the cyst contains eight sporozoites (*sp.z*), four sporal residua (*sp.r*), and a cystal residuum (*c.r*). *c.w*, cyst-wall. After Laveran and Mesnil [39], ×1000.

Genus 6. *Crystallospora*, Labbé, 1896. The dizoic spores have the form of a double pyramid (Fig. 66, *f*).

Type-species, *Crystallospora crystalloides* (Thélohan), from the intestine and pyloric caeca of *Motella tricirrata* of Roscoff.

FAMILY 4. POLYSPOROCYSTIDAE, Léger (Tribe *Polysporea*, A. Schn.). The oöcyst contains numerous spores (chlamydospores).

Genus 7. *Barroussia*, A. Schn., 1885. The monozoic spores are spherical, with smooth bivalve shell (sporocyst).

*B. ornata*, A. Schn., type-species, from the gut of *Nepa cinerea* (Fig. 64); *B. schneideri*, Léger, from the gut of *Lithobius impressus*; *B. caudata*, Léger, from the gut of *Lithobius martini*, is referred by Labbé to *Minchinia*.

Genus 8. *Echinospora*, Léger, 1897. The monozoic spores are oval, the bivalve sporocyst is spiny (Fig. 66, *c*).

Type-species, *E. labbei*, Léger, from the gut of *Lithobius mutabilis*. By Schaudinn and others this genus is united with the foregoing.

Genus 9. *Diaspora*, Léger, 1898. The monozoic spores are oval, the sporocysts are not bivalve, and have a micropyle at one pole (Fig. 66, *b*).

Type-species, *D. hydatidea*, Léger, from the intestine of the myriapod *Polydesmus*, in Provence.

By Schaudinn this genus is united with *Barroussia*.

Genus 10. *Adelea*, A. Schn., 1875. The dizoic spores are spherical or compressed, with smooth sporocysts (Fig. 65).

Type-species, *A. ovata*, A. Schn. (see p. 223, Figs. 55 and 56); others are *A. mesnili*, Perez (see p. 206, footnote); *A. akidium*, Léger; *A. tipulae*, Léger; *A. dimidiata* (A. Schn.), from the gut of *Scolopendra morsitans* (Fig. 65); and *A. simplex* (A. Schn.), from the gut of the larva of *Gyrinus*.

Genus 11. *Minchinia*, Labbé, 1896. The dizoic spores are oval, the sporocysts produced at each pole into two long filaments (Fig. 66, *a*).

Type-species, *M. chitonis* (E. R. L.), discovered by Lankester in the liver of *Chiton*. Allied species, not named, occur in a similar situation in *Patella* and *Trochus* (Labbé.) By Schaudinn this genus is united with *Adelea*.

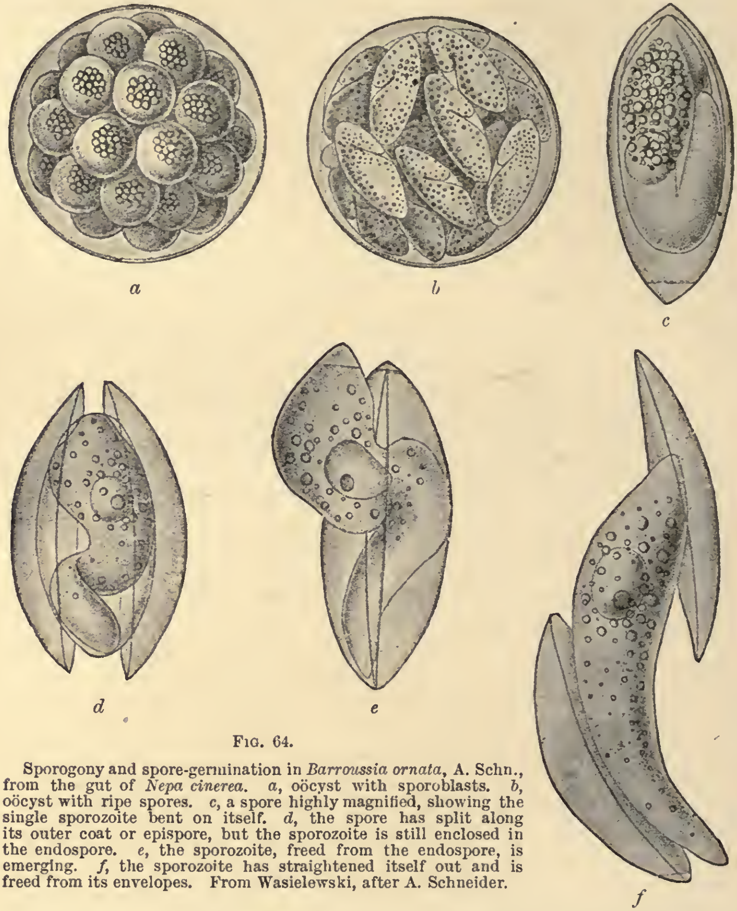

Fig. 64.

Sporogony and spore-germination in *Barroussia ornata*, A. Schn., from the gut of *Nepa cinerea*. *a*, oöcyst with sporoblasts. *b*, oöcyst with ripe spores. *c*, a spore highly magnified, showing the single sporozoite bent on itself. *d*, the spore has split along its outer coat or epispore, but the sporozoite is still enclosed in the endospore. *e*, the sporozoite, freed from the endospore, is emerging. *f*, the sporozoite has straightened itself out and is freed from its envelopes. From Wasielewski, after A. Schneider.

Genus 12. "*Benedenia*," A. Schn., 1875 (*Légeria*, Blanchard, 1900; *Eucoccidium*, Lühe, 1902). The spherical spores are trizoic. No schizogony.

Type-species, "*B.*" *eberthi* (Labbé), from the epithelium of the gut and other organs of *Sepia*[1] (Fig. 58).

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[1] The correct name of this species, commonly cited as *Benedenia octopiana*, A. Schn., is far from being settled. In the first place, as regards the generic name,

Genus 13. *Klossia*, A. Schn., 1875. The spherical spores are tetrazoic or polyzoic.[1]

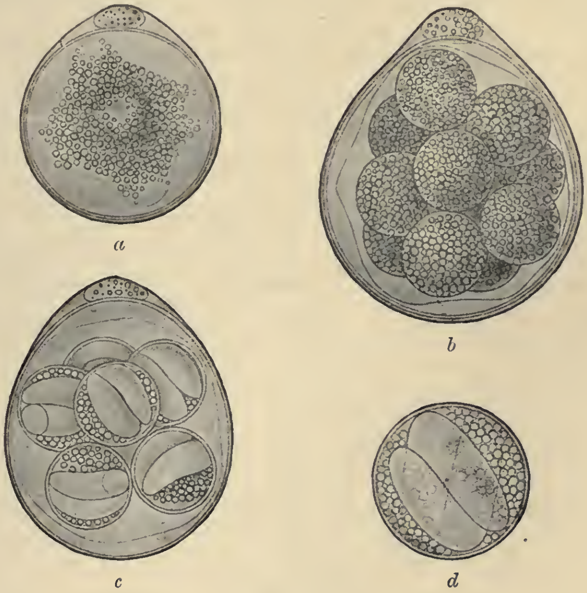

Fig. 65.

Sporogony of *Adelea dimidiata*, A. Schn. (par. *Scolopendra morsitans*). *a*, sporont encysted in a host-cell, and commencing to divide. *b*, the contents of the oöcyst have divided into a number of sporoblasts. *c*, oöcyst containing ripe spores. *d*, a ripe spore more highly magnified, showing the two sporocysts and the granular residual body. From Wasielewski, after A. Schneider.

The type-species is *K. helicina*, A. Schn. (Fig. 48), infesting the kidneys of various land-snails (*Helix* spp., *Succinea* spp.). The parasite and its life-

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many authors place the species in the genus *Klossia*. Assuming, however, that the trizoic condition is an adequate generic difference, the name *Benedenia* must nevertheless be changed on the ground of preoccupation, having been employed by Diesing in 1858 for a Trematode. Blanchard has proposed in its place the generic name *Légeria* (1900), but Labbé had already (1899) given this name to the genus of Gregarines previously termed *Dufouria* (see p. 200). As regards the specific name, Labbé terms the trizoic species, occurring in *Sepia*, *Klossia eberthi*, and retains the specific name *octopiana* of Schneider for a polyzoic species of *Klossia* occurring in *Octopus*. If two distinct species, inhabiting different hosts, were originally confused by Schneider under one name, this is certainly a useful reform.

Very recently Lühe [48*a*] has proposed the name *Eucoccidium* for *Benedenia*. He regards the name *Coccidium* as obsolete (see above p. 232, footnote), having been given to the sporogonous cycle of *Eimeria*. Since, therefore, "*Benedenia*" has only sporogony, he considers the name *Eucoccidium* appropriate to denote such a form. Lühe retains, however, the specific name *octopianum*, which is inappropriate if, as alleged, the species occurs in *Sepia* and not in *Octopus*.

[1] Mesnil [6] considers the genus *Klossia* to be normally tetrazoic, and states that in *K. helicina* the usual number of sporozoites is four, though it may exceptionally be as high as eight. He also throws doubt upon the alleged occurrence of 10-12 sporozoites in the spore of *K. octopiana*.

history were figured and described by Kloss in 1855, but not named by him—the first thorough account of any Coccidian. The spores contain five or six sporozoites. *K. soror*, A. Schn., from the kidney of the water-snail *Neritina fluviatilis*, is tetrazoic. *K. octopiana* (A. Schn.), Labbé, from the intestine of *Octopus* and *Eledone*, has ten to twelve sporozoites in the spore.

Genus 14. *Caryotropha*, Siedlecki, 1902. The spherical spores, about twenty in number, contain each twelve sporozoites. Unique species, *C. mesnilii*, Siedl. (Fig. 67), parasite of the clusters of spermatogonia of *Polymnia nebulosa*. Remarkable for its habitat, this species also shows some interesting peculiarities in its developmental phases (see pp. 223 and 225).

Genus 15. *Klossiella*, Smith and Johnstone, 1902. The subspherical spores are polyzoic and contain from thirty to thirty-four sporozoites. Unique species, *K. muris*, Sm. and Jnst., from the kidney of the mouse. The sporogonic cycle is found in the epithelium of the convoluted tubules. Another form, representing the schizogonic cycle, apparently, is found in the glomeruli. The very large number of sporozoites is a remarkable feature of this species.

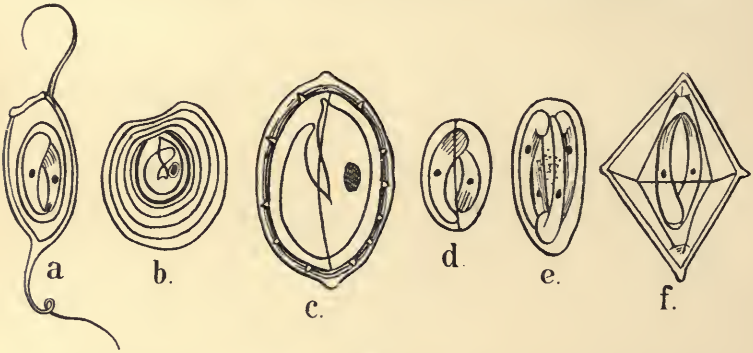

Fig. 66.

Spores of various Coccidian genera. *a*, *Minchinia chitonis* (E. R. L.), (par. *Chiton*); *b*, *Diaspora hydatidea*, Léger (par. *Polydesmus*); *c*, *Echinospora labbei*, Léger (par. *Lithobius mutabilis*); *d*, *Goussia motellae*, Labbé; *e*, *Diplospora* (*Hyaloklossia*) *lieberkühni* (Labbé), (par. *Rana esculenta*); *f*, *Crystallospora crystalloides* (Thél.), (par. *Motella tricirrata*). *b* and *c* after Léger, the others after Labbé.

Doubtful genera are:—

*Hyaloklossia*, Labbé, 1896, characterised by polysporous oöcysts with oval spores which are either dizoic or tetrazoic. The type-species, *H. lieberkühni* (Labbé), from the kidney of *Rana esculenta*, has been found, however, by Laveran and Mesnil [40] to be a *Diplospora* (*vide ante*, p. 231); but another species, *H. pelseneeri*, Léger, is described from the kidney of *Tellina*, which appears to conform to Labbé's generic definition, although the latter was founded on a mistaken observation.

*Goussia*, Labbé, 1896, which differs from *Coccidium* by its bivalve spores (Fig. 66, *d*), opening like a pea-pod (Gallicé *gousse*). The genus, as thus characterised, includes, according to Labbé, eight species, all infesting the intestine or liver of various fishes. By other authors the genus is united with *Coccidium*.

*Bananella*, Labbé, 1895, founded for *B. lacazei*, Labbé, from *Lithobius*,

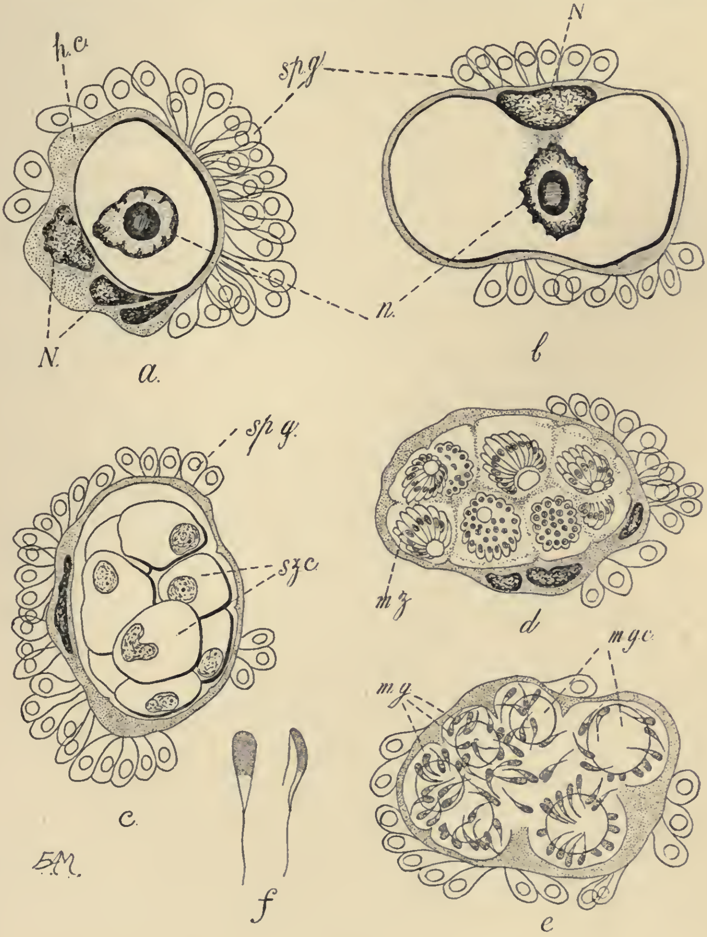

Fig. 67.

Phases of *Caryotropha mesnilii*, Siedl. (par. *Polymnia nebulosa*). *a*, young schizont in a cluster of spermatogonia; the host-cell (represented granulated) and two of its neighbours are greatly hypertrophied, with very large nuclei, and have fused into a single mass containing the parasite (represented clear, with a thick outline). The other spermatogonia are normal. *b*, full-grown schizont enclosed in the hypertrophied host-cell, with an enormous nucleus, which appears to be connected with the nucleus of the parasite by a band of granules. *c*, intracellular schizont divided up into schizontocytes. *d*, each schizontocyte giving rise to a cluster of merozoites arranged as a "corps en barillet." *e*, intracellular microgametocyte divided into microgametocytes of the second order, each of which is forming numerous microgametes. *f*, microgametes in front and side view. *spg*, spermatogonia; *h.c*, host-cell; *N*, nucleus of host-cell or cells; *n*, nucleus of parasite; *szc*, schizontocyte; *mz*, merozoites; *mgc*, microgametocytes of the second order; *mg*, microgametes.

and characterised, according to its founder, by forming three, exceptionally four, spores ; hence made the type of a tribe *Trisporea.* Schaudinn, Blanchard, and others regard the trisporous condition as an anomaly, and place the species under *Coccidium.*

*Rhabdospora*, Laguesse, 1895 ; *Gonobia*, Mingazzini, 1892 ; *Pfeifferella*, Labbé, 1899 ; *Molybdis*, Pachinger, 1886 ; *Cretya*, Mingazzini, 1892 ; and perhaps also *Gymnospora*, Moniez, 1886, probably all of which represent the schizogonous generations of species of *Coccidium* and other genera. For full details concerning them the reader is referred to Labbé [4].

*Branchiocystis*, Burchardt, 1900 (*Jen. Zeitschr. f. Nat. wiss.* 34, pp. 779-784, pl. xix. figs. 9-11, and xx. figs. 1-9), a genus founded for *B. amphioxi*, a "Coccidium" parasitic on the epithelium of the gill-bars of Amphioxus. It was found to be seldom absent in Amphioxus material from Naples and Messina, and often occurred in abundance, affecting especially the gill-bars at the level of the apex of the liver. The parasite appears as a rounded or oval body, 10-14 $\mu$ in diameter, lodged in the flagellated epithelium of the broad sides of the gill-bars. Some of these bodies appear homogeneous, without nucleus (?) ; others contain a number of oval or rounded "sporoblasts," 2-2·5 $\mu$ in diameter, which become sausage-shaped bodies.

It is difficult to see why the author should consider *Branchiocystis* a Coccidian. The description does not render it possible to place it near any of the recognised genera of Coccidia. The figures given remind one more of the *Glugeidae* amongst Myxosporidia than of any true Coccidian, and it is perhaps in or near the genus *Pleistophora* (p. 297) that this parasite would be correctly placed.

*Coccidioides*, Rixford and Gilchrist, 1897, for *C. immitis*, R. and G., a problematic organism occurring as a parasite of man, and up to the present observed only in America. The infection, or rather contagion, is acquired by the skin, whence the parasites spread into the lymphatics and invade other organs. The malady caused by the parasite may be chronic or acute, and in the latter condition it is fatal in a short time. The characteristics of the disease are very similar to those of miliary tuberculosis, an immense number of minute nodules being formed in all the viscera. In each nodule one or two parasites are found, either free or lodged in a giant cell. The parasites have the form of "rounded protoplasmic masses, 20, 50, 60, or 80 $\mu$ in breadth, surrounded by a thick enveloping membrane. Their multiplication . . . is effected by a series of bipartitions which go on within the membrane. The latter then bursts and sets free the young parasitic elements, which grow *in situ*, or are carried away by the blood or lymph" (Blanchard). Several forms of the parasite have been described, and have even received distinct names. A full account of them will be found in Blanchard [30], who considers that they are Sporozoa, but not to be included in the order Coccidiidea.

## ORDER 3. **Haemosporidia.**

The Haemosporidia are a group of Sporozoa adapted to a very special mode of parasitism, and therefore limited in habitat and occurrence. They exhibit, however, an interesting range of variations, both in morphological structure and in adaptation to their special life-conditions. Their distinctive features are as follows. They are parasitic usually upon the red blood-corpuscles, sometimes also upon other cells, of Vertebrata. The trophozoite is *endoglobular*, *i.e.* intracellular, in situation, and may remain so throughout the whole trophic period, or may quit the host-cell and become free in the blood-plasma after reaching a certain stage of growth. The endoglobular forms are very commonly amoeboid, but those which become free have definite body-contours, and resemble tiny gregarines of elongated form and worm-like appearance, which when liberated from the blood-corpuscle are actively motile. The life-cycle shows an alternation of generations similar to that occurring in Coccidia. In all cases, probably, non-sexual reproduction by means of *schizogony* continued through many generations serves to multiply the parasites within the host, and is then followed by the formation of gametes, which conjugate to produce zygotes or sporonts. Each sporont is at first motile, and seeks out a suitable position in which to become encysted as an oöcyst. It then undergoes *sporogony* to form a number of minute germs, which are always naked gymnospores or sporozoites, never enclosed in sporocysts. In many forms, perhaps in all those parasitic upon warm-blooded animals, the entire sexual cycle takes place in an *intermediate host*, an invertebrate animal of blood-sucking habits, upon which the sporont is actively parasitic, and by which fresh vertebrate hosts are inoculated with the germs of the parasite.

Our scientific knowledge of the Haemosporidia is of extremely recent date, and begins with the discovery, by Lankester, in 1871, of the parasite of the frog's blood, which in 1882 he named *Drepanidium* (=*Lankesterella*) *ranarum*, and recognised as a member of the Sporozoa. At the latter date Laveran, then a military doctor at Constantin in Algiers, discovered the malarial parasite in human blood. He described all its characteristic stages—amoebula, rosette, crescent, sphere, and flagellated body—and saw in it the cause of the disease, but it was many years before his ideas became generally accepted. Laveran did not at first recognise the true nature of the parasite he had discovered, but regarded it as a vegetable organism and named it *Oscillaria malariae.* Metschnikoff was the first to place it amongst the Sporozoa, under the generic designation *Haematophyllum* (1887); it had already, however, been named *Plasmodium* by Marchiafava and Celli in 1885. Our knowledge of these organisms was further advanced by the studies of Danilewsky, who gave them as a class the name Haemosporidia or Haemocytozoa, and by other investigators. In 1894 Labbé brought forward detailed and extended researches upon these parasites, and described many new forms. The concluding years of the nineteenth century have brought a very rapid increase in our knowledge of the malarial parasites, and the labours of Ross, Grassi, and many others have revealed their complete life-history, a chapter of biology of the greatest practical importance as well as of scientific interest. At present it is amongst the Haemosporidia of cold-blooded Vertebrata that researches are most needed.

(*a*) *Occurrence and Habitat.*—The Haemosporidia are found commonly as blood-parasites in mammals, in birds, and in all the existing orders of reptiles, except perhaps the Rhynchocephala. Amongst amphibia they appear to occur abundantly in the frog, at least, which has been credited with harbouring no less than five species, distributed amongst four genera, of these parasites; but it is highly probable that improved knowledge will bring about reductions in this list. From Urodela, on the other hand, only doubtful species have been recorded. In fishes also Haemosporidia were generally considered to be conspicuous by their absence, but very recently Laveran and Mesnil [79, 79*a*] have described species infesting rays, soles, and blennies respectively. If we except the cases where a part of the life-cycle is passed through in an intermediate host, there is no record of their occurrence in Invertebrates, with the exception of one very doubtful species (*Haemogregarina nasuta*, Eisen) stated to occur in the walls of the blood-vessels and the mesentery of an Annelid (*Eclipidrilus frigidus*).

The principal habitat of Haemosporidia is the red blood-corpuscles of their hosts, but they may be found also in the leucocytes, and in the cells of certain organs, especially the spleen and bone-marrow. It is not uncommon for the reproductive phases of the parasite in the vertebrate body to be rare or absent in the blood of the peripheral circulation, in which only growing trophozoites or gametocytes are to be found, while the "rosettes" and other stages of schizogony occur only in the more slowly flowing blood of the brain, liver, kidney, and other viscera. The situation of the endoglobular parasite is always *within* the blood-corpuscle or cell it attacks,[1] and not, as supposed originally by Laveran, merely one of attachment to the corpuscles. In the case of the forms parasitic upon Vertebrata other than mammals, the nucleus of the haematid is often displaced by the parasite, proving clearly its internal position. Occasionally the nucleus itself may be attacked; a good example of this is seen in the form parasitic upon various species of *Lacerta*, which from its effects upon the nucleus of the host-cell has been termed *Karyolysus lacertarum*. In blood-corpuscles infected with *Karyolysus*, the nucleus becomes hypertrophied and divides amitotically into two or more fragments, which ultimately degenerate (Fig. 76).

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[1] The view of Laveran that the parasites are attached ("accolés") to the corpuscle has recently been revived and supported by Argutinsky [61, 1901], but his statements have been criticised and contradicted by Schaudinn [94*a*], who is strongly in favour of the view put forward above.

In the sub-order Acystosporea the parasite retains the endoglobular or intracellular situation throughout the whole endogenous generation, except for the brief period during which the merozoites are seeking fresh corpuscles to attack. But in the sub-order Haemosporea the parasite leaves its first host-cell and becomes free in the blood-plasma. It then penetrates other corpuscles, which it may abandon again, but as a rule it comes to rest finally within a corpuscle or cell, and undergoes schizogony in this situation, though sometimes even the reproductive stages may be free in the spleen-pulp or bone-marrow.

The effects produced by Haemosporidia upon their hosts seem to differ markedly in the case of cold-blooded and warm-blooded animals. In the former there is no evidence that these parasites, however numerous, produce any pathological effect upon their hosts at all. But in birds and mammals they cause fevers and agues of various kinds, of which those that trouble the human species are naturally the best known. The varieties of malarial fevers and their symptoms will be found described in medical treatises, but a few points may be briefly summarised here. At least three types of fever are generally recognised, each caused by a distinct form of parasite (see below, p. 243)—the two so-called benign intermittent fevers, tertian and quartan ague, and the pernicious aestivo-autumnal fever or tropical malaria. In each case the parasite is introduced into the human body by the bite of a mosquito, and not, so far as is known, in any other way. After a period of incubation, varying from six to twelve days, according to the species of parasite, the fever makes its appearance. In the benign forms the feverish symptoms appear at regular intervals, dependent on the time occupied by a complete reproductive cycle of the parasite. Thus in the parasite of tertian ague the schizogony takes forty-eight hours, and the fever recurs every other day. In quartan ague the schizogony takes seventy-two hours, and the attacks of fever recur once every three days. There may, however, be double or triple infections, the result of distinct inoculations; or again there may be mixed infections of the two forms, so that distinct generations of the parasites occur contemporaneously in a given patient, producing every possible variation in the frequency of the attacks of fever. In pernicious malaria, on the other hand, the sporulation takes place irregularly, and the fever is consequently irregular or continuous in its manifestations. In all cases the fever coincides in its appearance with the actual sporulation of the parasite, when vast numbers of merozoites are set free in the blood, and are attacking fresh, healthy corpuscles. The result of the rapid multiplication of the parasite in the blood, and the consequent destruction of the corpuscles, is a condition of anaemia which tends to produce general cachexy, and may terminate fatally. At the same time the melanin-granules produced by the parasite, and dispersed in the blood when the sheltering corpuscle disintegrates and the merozoites scatter (see below, p. 245), become deposited in the spleen and liver, which become hypertrophied, and also in the lungs, kidneys, and brain, causing a pigmentation of these organs. In pernicious malaria death may ensue from the accumulation of the parasites in the capillaries of the brain to such an extent that the circulation is hindered or completely blocked. Finally, it should be mentioned that the fevers may be acute or chronic, and that in the latter condition the disease may be masked or latent for a considerable period. What exactly happens to the parasite during this time is now the only obscure part of its life-history.

Fevers similar to malaria appear to be produced in birds and in various mammals by Haemosporidian parasites. In birds, according to Macallum [84], characteristic changes take place in the internal organs, resulting from the destruction of blood-corpuscles and the deposition of pigment. The spleen and liver are the parts chiefly affected; the bone-marrow and other organs less so. In cattle an acute and rapidly fatal disease, the so-called Texas-fever ("Tick-fever," "Tristeza," "Redwater," etc.), is produced by *Piroplasma bigeminum*, manifesting itself in high body-temperature, loss of appetite, and jaundice of the sclerotics, accompanied by general dulness and emaciation, and in many, though not in all cases, by pronounced haemoglobinuria, the urine being the colour of port-wine. In horses a fever similar to malaria is produced by *Piroplasma equi*, and in dogs *Piroplasma canis* is the cause of the so-called "malignant jaundice," very similar in its symptoms to Texas-fever in cattle. Interesting discoveries with regard to the life-histories of these parasites are probably to be expected in the near future.

(*b*) *Morphology and Life-history.*—The forms that have been most fully worked out, and of which the life-histories are best known, are those infesting the human blood. They may therefore serve as types of the structural and developmental characteristics of the whole order, and the distinctive features of other forms will be described briefly afterwards.

It is still a matter of controversy how many species of these parasites occur in the blood of man. Their discoverer, Laveran, regards them all as one species; some authorities, on the other hand, believe in the existence of as many as five different kinds.

The majority of experts, however, are agreed in recognising three distinct species, divided amongst two different genera.[1] These are (1) *Laverania malariae*, Gr. et Fel., the parasite of pernicious malaria; (2) *Plasmodium malariae* (Lav.), the parasite of quartan ague; and (3) *Plasmodium vivax* (Gr. et Fel.), the parasite of tertian ague. The following account refers more especially to the first of these, but the peculiarities which characterise the other two will be briefly mentioned by way of comparison.[2]

The minute sporozoites, introduced into the human blood by the bite of a mosquito, attack and penetrate red blood-corpuscles, probably in a way similar to the infection of epithelial cells by Coccidian parasites. Each sporozoite ("exotospore," Lankester)[3] is slender, almost filamentous in form, the body sharply pointed at each end, with a thicker central portion in which the nucleus is lodged (Fig. 68, XIX). Within the blood-corpuscle the sporozoite rounds itself off and develops into an amoeboid trophozoite, which grows at the expense of the blood-corpuscle until it nearly fills it (Fig. 68, I-V). The youngest amoebulae are without any pigment, but usually contain, in fixed and stained preparations, a conspicuous vacuole, giving the parasite the so-called ring-form. With further growth the vacuole disappears, and grains of pigment termed *melanin*, representing, probably, an excretory product, are formed in the body of the parasite and collect towards the centre near the nucleus. When full-grown the trophozoite acquires a rounded form and is now a ripe schizont ("sporulating body," "sporocyte"), ready to reproduce itself by schizogony (Fig. 68, 6). The nucleus divides to form a variable number of daughter nuclei, which travel to the periphery (Fig. 68, 7, 8). The protoplasmic body becomes divided up into a corresponding number of segments, the merozoites ("enhaemospores," Lankester), centred round a small mass of residuary protoplasm, in which all the pigment-granules are deposited (Fig. 68, 9). This characteristic form of the parasite, known as the rosette-stage ("corps en rosace"), corresponds to the so-called "Eimerian cysts" of the Coccidia. When the schizogony is complete, or, it may be, during the initial stages of this process, the exhausted blood-corpuscle breaks up,

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[1] See also footnote to p. 267.

[2] Since the account here given of the life-cycle of the malarial parasites was written, the very important monograph of Schaudinn [94*a*] upon the tertian parasite has come to hand, just as the proofs of this article are going to be paged. It is therefore, unfortunately, not possible to introduce any of Schaudinn's figures; but had his memoir appeared earlier, some portions of Fig. 68 might have been made less diagrammatic.

[3] Numerous terminologies have been suggested, and are in use, for the phases of the malarial parasite; the most recent is that suggested by Lankester, in *Nature*, vol. lxv. No. 1691 (27th March 1902). The scientific terminology of Schaudinn, already introduced above for the Coccidia, is employed here, but reference is also made to other names applicable specially to the various stages of the malarial parasites.

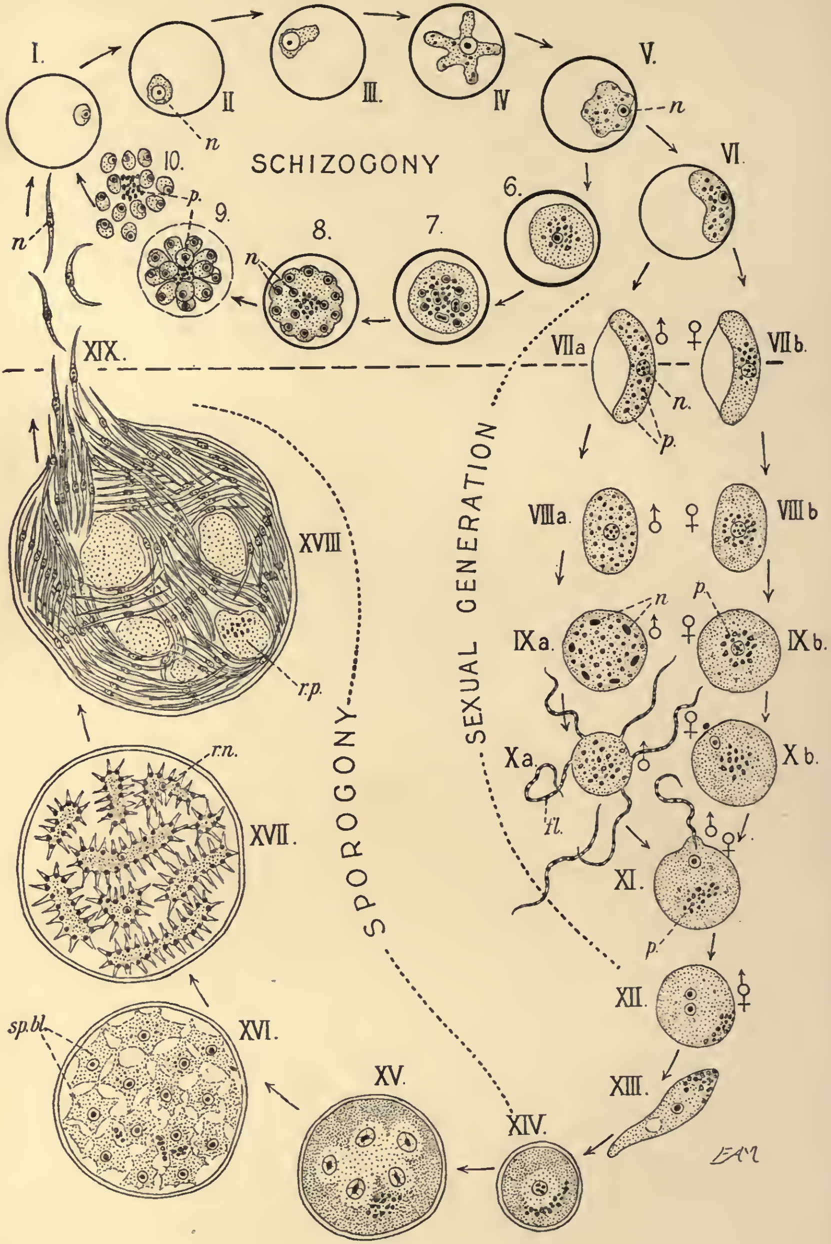
I.
II
n
III.
IV
V.
n
VI.
SCHIZOGONY
10.
p.
9.
8.
7.
6.
n
n
XIX.
VIIa
♂
♀
VIIb.
n.
p.
SEXUAL GENERATION
VIIIa.
♂
♀
VIIIb
n
p.
IXa.
♂
♀
IXb.
XVIII
r.p.
Xa.
♂
♀
Xb.
fl.
r.n.
XVII.
SPOROGONY
XI.
♂
♀
p.
XII.
⚥
sp.bl.
XVI.
XIII.
XV.
XIV.
EAM

Fig. 68.

and the merozoites are set free in the blood-plasma (Fig. 68, 10), abandoning the residuary protoplasm, which becomes disintegrated, scattering its contained pigment. The merozoites behave as did the sporozoites from which they are descended; that is to say, they attack and penetrate fresh blood-corpuscles, and develop in their turn into schizonts which produce fresh generations of merozoites over again by the method of schizogony.

The endogenous cycle is similar in all essential features in the three species of the parasites of man, but each of them has its own distinctive characteristics. The amoeboid movement is most active, and continues longest, in *Plasmodium vivax*, most sluggish in *P. malariae*. In *Laverania* the movements are very lively in the youngest, unpigmented stage. In all they slow down as the parasite approaches its full size. They differ markedly also in their effects on the blood-corpuscle. Those attacked by *Plasmodium malariae* diminish in size but retain their normal colour. Corpuscles attacked by *P. vivax*, on the contrary, increase considerably in size and become paler. The effect produced by *Laverania* varies greatly; the corpuscle is sometimes increased, sometimes diminished in size, and the colour may be lessened or heightened in tint.

Fig. 68.

Diagram of the complete life-cycle of the parasite of pernicious malaria, *Laverania malariae*, Gr. et Fel. The stages on the upper side of the dotted line are those found in human blood; below the dotted line are seen the phases through which the parasite passes in the intermediate host, the mosquito. I-V and 6-10 show the schizogony. VI-XII, the sexual generation, which at VII splits into two lines (*a*) male and (*b*) female, to be united again by conjugation (XI and XII). XIII, the motile zygote. XIV-XIX, sporogony. I-III, young amoebulae in blood-corpuscles, the two last showing the ring-form (which is, however, not quite correctly drawn; see p. 246). IV, older, actively amoeboid trophozoite. V, still older, less amoeboid trophozoite. 6, mature schizont. 7, schizont with nucleus dividing up. 8, young rosette stage. 9, fully-formed rosette stage; merozoites round a central residual mass of protoplasm containing the pigment, and blood-corpuscle beginning to break down. 10, merozoites free in the blood by breaking down of the corpuscle. VI, young indifferent gametocyte. VII*a*, male crescent. VII*b*, female crescent. VIII *a* and *b*, the gametocytes becoming oval. IX *a* and *b*, spherical gametocytes; in the male (IX *a*) the nucleus has divided up. X *a* and *b*, formation of gametes; in the male (X*a*) the so-called flagella or male gametes (*fl*) are thrown out, one of them is seen detached; in the female (X*b*), a portion of the nucleus has been thrown out. XI, a male gamete penetrating a female gamete at a cone of reception formed near the nucleus. XII, zygote with two pronuclei in proximity. XIII, zygote in the motile stage (vermicule or oökinete). XIV, encysted zygote (oöcyst). XV, commencing multiplication of the nuclei in the oöcyst. XVI, oöcyst with numerous sporoblasts. XVII, commencing formation of sporozoites; the nucleus of each sporoblast has divided to form numerous nuclei, each of which is growing out in a little tongue of protoplasm to become a sporozoite, but a few nuclei remain behind as residual nuclei. XVIII, full-grown oöcyst crammed with ripe sporozoites; on one side the cyst has burst and the sporozoites are escaping. XIX, free sporozoites, showing their changes of form. *n*, nucleus of the parasite; *p*, melanin pigment; *fl*, "flagella"; *sp.bl*, sporoblasts; *r.n*, residual nuclei; *r.p*, residual protoplasm. (Chiefly after Neveu-Lemaire, from whom the plan and arrangement of the different stages is borrowed, with slight modifications; details of the figures are founded on the figures of Grassi, Schaudinn (Leuckart's *Zoologische Wandtafeln*), Ross, and others.)

Schaudinn [94*a*] has recently studied the very active movements of the sporozoites, and has observed the penetration of blood-corpuscles by them, and by merozoites, in the case of the tertian parasite. He finds that, as in the Coccidia, the sporozoites perform movements of flexion and of peristaltic or euglenoid contraction, and that in addition they have the power of gliding rapidly forward, with formation of a trail of gelatinous substance. All three varieties of movement go on at the same time. The penetration of the corpuscle takes about three-quarters of an hour, more or less, and is effected in a manner very similar to that described above (p. 211) for Coccidia. The movements of the merozoites are similar to those of the sporozoites, but less active, and they may also show feeble amoeboid movements.

Opinions still differ considerably as to the true structure and significance of the very characteristic ring-stage of the endoglobular parasite. Some authorities regard it as truly ring-like in structure, the result of the union of two horn-like outgrowths or pseudopodia. Amongst recent writers this view is supported by Ewing [66]. But most authorities consider the ring-like appearance as merely the optical section of a vesicular structure. Even then it is far from clear whether the vesicle is a vacuole or whether it is simply the enlarged nucleus, distended by fluid nuclear sap and containing a relatively small quantity of chromatin. The latter alternative is, according to Argutinsky [61, 1902] and others, the true interpretation of this stage. Argutinsky considers, however, the distended condition of the nucleus to be merely the artificial result of unsuitable methods of preserving these parasites as microscopic objects. He states that if blood-films are treated with fixatives *before* being dried, nothing is seen of any "ring-forms," but the nucleus appears as an even spherical mass of chromatin, not surrounded by any clear space intervening between it and the protoplasm of the body; if, on the contrary, the blood-film be dried before fixation, according to the method of procedure most commonly in vogue, the result is a deformation of the tiny parasite, producing the ring-like appearance. On the other hand, Schaudinn [94*a*] gives a very different account of the ring-form in the case of the tertian parasite. He finds that it does not occur in the development of the gametocytes, but that it is a constant stage in the growth of the schizonts. In the latter case it appears in the youngest amoebulae as a vacuole situated close to the nucleus. The vacuole grows rapidly in size, causing the parasite to have the form of a signet-ring, as commonly described, the nucleus being on one side of the ring. When the ring-stage is fully developed it is difficult to say whether the vacuole is still closed in, above and below, or whether the body does not become truly ring-like. Schaudinn regards this vacuole as nutritive in function, connected with the absorption of food-substance, and serving to increase the body-surface of the parasite; its appearance close to the nucleus supports this interpretation; and its presence in young schizonts, but not in young gametocytes, is correlated with the fact that the former grow twice as fast as the latter.

According to Billet [64], the endoglobular malarial parasite has constantly at a certain stage of its growth an elongated form, coiled round within the corpuscle. Billet terms this the Gregariniform stage, and considers that it represents the haemogregarine phase of the Gymnosporidia. It remains to be seen to what extent such a stage is of constant occurrence. According to Argutinsky's figures and descriptions [61, 1902] of the tertian parasite, it frequently has "an elongated vermiform shape," which is to be regarded as merely one of the many forms which result from its very great amoeboid activity, and this author shows that even the nucleus shares, to a certain extent, in the changes of body-form. Schaudinn's detailed monograph [94*a*] of the tertian parasite contains nothing to support Billet's view.

The schizogony is most easy to study in the two species of *Plasmodium*, since in them it commonly takes place in the peripheral circulation, and rosette-stages can be obtained in a drop of blood from the finger or elsewhere. In *Laverania*, on the other hand, the sporulation goes on, as a rule, in the internal organs, and its stages are difficult to obtain. The multiplication of the nuclei in the schizont commences by a primitive form of mitosis, but as the nuclei increase in number, the method of division becomes a simpler type of multiple nuclear fission (Schaudinn [94*a*]). The schizonts are distinguished by trifling differences of pigmentation in the three species, and also by variations in the process of sporulation. In the quartan parasite the rosettes have a form which has been compared to that of a daisy, and are relatively few, from nine to twelve in number. In the tertian species the merozoites are more numerous, usually from twelve to twenty-four in number, and the corresponding stage has more the form of a mulberry. In *Laverania* the forms of the rosettes, and the number of the merozoites in each, are very variable. Most characteristic, however, is the length of time required by each species to complete a generative cycle. In *P. malariae* a schizogonous generation, from sporozoite (or merozoite) to merozoite, occupies seventy-two hours; in *P. vivax*, forty-eight; while in *Laverania* it is twenty-four hours or of irregular duration.

By repeated schizogony the numbers of the parasites in the blood increase by geometrical progression, in a way similar to the Coccidia in an infected epithelium, until a very large number of the corpuscles are infected and destroyed. Apparently the only check to the multiplication of the parasite is to be found in the activity of the leucocytes, which sometimes capture and destroy a merozoite or other free stage. It is evident that reproduction at this rate could only continue indefinitely in the *ichor* of an infinite host. In the blood of an ordinary mortal of limited capacities the results are most dangerous and even fatal. Provision is therefore soon made for the transference of the parasite to fresh hosts and new spheres of activity by the development of certain merozoites into sexually differentiated schizonts or gametocytes, the appearance of which is the prelude, as in Coccidia, to reproduction by sporogony. In *Laverania* the gametocytes are distinguished at once from ordinary schizonts by their peculiar form, like that of a sausage, slightly bowed, and considerably exceeding in length the diameter of the blood-corpuscle, the remains of which are seen in the concavity of the gametocyte (Fig. 68, VII*a*, VII*b*). Hence these forms of the parasite, very characteristic of pernicious malaria, are commonly known as "crescents." The gametocytes are not all alike, however, but can be separated into two categories, distinguished, though not always very sharply, by the arrangement of the pigment-granules. In the male crescents or microgametocytes the grains of pigment are scattered evenly in the cell-body; in the female crescents or macrogametocytes the pigment is aggregated at the centre, surrounding the nucleus. The crescents appear to originate in the spleen and bone-marrow, but when full-grown they are found in the peripheral circulation. As they approach maturity the crescent-shaped gametocytes undergo a change of form, becoming first oval, then spherical, and free themselves in the final stage from the remains of the blood-corpuscle (Fig. 68, VIII *a* and *b*, IX *a* and *b*). The changes from crescent to sphere may take place in the human blood, or not until transference to the intermediate host, the mosquito, has been effected. In no case, however, do the gametocytes get beyond the spherical stage in the human body.

The two species of *Plasmodium* are at once distinguishable from *Laverania* by the fact that the gametocytes do not take on the form of crescents, but have the same rounded shape as the ordinary schizonts. The various forms of the tertian parasite have recently been studied in great detail by Argutinsky [61] and Schaudinn [94*a*], whose results are, in the main, in harmony. (1) The schizonts are about 10 $\mu$ in diameter, with a nucleus usually situated excentrically, and containing at first a single mass of chromatin, later a number of chromatin granules held in an even achromatic network, the whole being surrounded by a delicate alveolar border (*sic* Schaudinn; Argutinsky characterises the nucleus of the schizont as vesicular). (2) The macrogametocytes are much larger (12-16 $\mu$ in diameter), when full-grown, than the schizonts, and much less amoeboid during earlier stages of growth. Their protoplasm is dense and stains deeply, and their grains of pigment are two or three times as large, and fully twice as numerous, as those of the schizont. The nucleus, situated at the periphery, is oval or elongated in form, with grains of chromatin in the nodes of an alveolar framework. (3) The microgametocytes are distinguished in all stages by their very large chromatic nucleus, containing coarse grains of chromatin, and situated centrally. The protoplasmic portion of the body is feebly developed as compared with the two foregoing, and it is less dense and stains a much lighter tint. It is scarcely at all amoeboid at any stage. The melanin-pigment is abundant and the grains appear larger than in the macrogamete, but according to Schaudinn this is an optical illusion. Schaudinn considers the differences between (2) and (3) to be adapted to their rôle in development. The macrogamete, like an ovum, has to provide for posterity, hence its large bulky protoplasmic body. In the microgametocyte, only the nuclear substance passes on into the next generation, hence the protoplasmic body is to a large extent atrophied, while the nucleus is greatly developed.

The stages in the origin and growth of the gametocytes are still somewhat obscure. Mannaberg derived the crescent-form from a syzygy, *i.e.* the union and fusion of two amoebulae, and more recently Ewing [66] has maintained that unions of this kind take place between amoebulae.

The latter author describes the conjugation and fusion of ring-stages in pairs within the blood-corpuscles. Wright [98] also supports the view that the crescents arise from a syzygy of amoebulae within a doubly-infected corpuscle. The analogy of the life-histories of other Haemosporidia or Sporozoa affords no support to these statements, and the appearances upon which they are based might equally well be interpreted as stages in the fission of an amoebula or young gametocyte. Recently Schaudinn [94*a*] has traced all stages in the development of the gametocytes of the tertian parasite from the merozoites, so that the notion that the former arise from fusions of amoebulae must be regarded as an exploded idea.

The intermediate host necessary for the propagation of the parasites of malaria in man is a gnat or mosquito, belonging to the genus *Anopheles*. Up to the present no other means of propagating the disease has been discovered than through the agency of these insects. If a human being suffering from malaria is bitten by an *Anopheles* mosquito (it is only the female gnats that suck blood), the mosquito draws into its stomach various stages of the parasite along with the blood. Young amoebulae, full-grown schizonts, rosettes, crescents, all alike may be swallowed by the mosquito, but with different results. All stages of the schizogonous cycle are digested in the mosquito's stomach along with the blood corpuscles. The gametocytes alone are able to resist the action of the digestive juices, and to continue their development further. Freed from the last remnants of the blood-corpuscle in which they grew up, they assume the spherical form, if they have not already done so, and proceed to give rise to the gametes. The maturation of the gametes and their subsequent conjugation take place in the stomach of the mosquito.

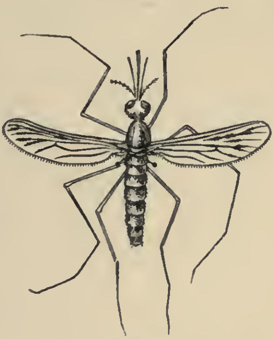

FIG. 69.

*Anopheles claviger*, Fabr. (After Grassi.) × about 4.

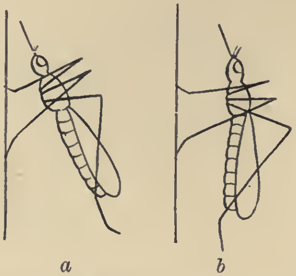

FIG. 70.

Diagrams to show the positions assumed when at rest by—*a*, *Anopheles* ; *b*, *Culex*. (After Neveu-Lemaire.)

The relation of the Haemosporidia to their intermediate hosts is one of those finely-adjusted bionomical adaptations so frequently observed in the life-histories of parasites. For if a malarial patient be bitten by a mosquito of any other genus than *Anopheles*—by a species of *Culex*, for example—then not only the schizonts, but also the gametocytes, are digested by it. *Culex*, on the other hand, is the intermediary for the *Haemoproteus* (=*Proteosoma*) of birds, and when it bites a bird infected with this genus of parasites, it digests all the stages except the gametocytes. *Culex*, in fact, stands in the same relation to the malarial parasites of birds, as *Anopheles* to those of man. Should an *Anopheles*, on the other hand, bite a bird infected with *Haemoproteus*, it will digest every stage of the parasite, gametocytes and all.[1]

In the spherical microgametocyte ("sperm-mother-cell," Lankester) the nucleus breaks up and the fragments of chromatin travel to the periphery (Fig. 68, IX*a*). From Schaudinn's observations upon *Haemoproteus* it would appear that a karyosome is left in the centre of the body, as in *Coccidium*. The surface of the body grows out into long thread-like processes, usually four to six in number, each extremely motile and resembling in its movements a flagellum. Hence the parasite at this stage is known as the *Polymitus* form, since it was regarded by some earlier observers as a Flagellate belonging to that genus. The entire chromatin substance of the microgametocyte passes into the so-called flagella, which are in reality the microgametes ("spermatozoa," Lankester). They are formed very rapidly, and by their active movements soon become detached from the body of the gametocyte, which, like that of the Coccidia, is completely enucleated, except for its karyosome, and perishes as residual protoplasm, together with the contained melanin-granules. Each microgamete is a slender filament, slightly thickened in its middle portion, where is lodged the chromatin which composes the greater part of its substance. Like the microgametes of *Adelea* and *Benedenia* amongst Coccidia, it has no true flagella, but progresses actively by serpentine movements of the body in quest of a macrogamete.

In the macrogametocytes also the development is on the same type as in Coccidia. The schizogony is completely suppressed, and each macrogametocyte becomes a macrogamete after having gone through a process of maturation by ejecting a portion of its nucleus (Fig. 68, X*b*). It is then ripe for fertilisation.

The gametes conjugate in a manner essentially similar to that described above in Coccidia. After the microgamete has penetrated the macrogamete, the two pronuclei fuse into a single nucleus (Fig. 68, XI, XII). The zygote at first has the form of a sphere, but soon after fertilisation it becomes elongated and spindle-shaped, and grows into a small worm-like, or rather gregarine-like body, which is actively motile, and has been termed a *vermicule* by many writers (Fig. 68, XIII). Since it corresponds exactly to the zygote of the Coccidia, but does not form an oöcyst immediately after fertilisation, Schaudinn has proposed for it the name of *oökinete*, by which it is now generally known. The movements of the ökinete are very similar to those of a sporozoite, and consist of locomotion by gliding forwards, combined with flexions and peristaltic contractions of the body (Schaudinn [94*a*]).

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[1] Schaudinn believes, with Grassi, that in some cases the *Anopheles* may be naturally immune against the malarial parasite, and that such immunity, if acquired by a whole race of the mosquito, would account for the disease having died out in localities where it was formerly abundant, as in the eastern counties of England, for example.

The oökinete by its own activity bores through the epithelial lining of the stomach of the mosquito, and comes to rest in the tissues immediately below the epithelium. Here it becomes rounded off again in shape, and a delicate cyst-envelope of disputed origin becomes formed round it (Fig. 68, XIV). The zygote is actively parasitic upon its new host, and commences to grow considerably in size, bulging out the stomach-wall towards the body-cavity. The oökinete has now become the oöcyst ("spore-cyst," Lankester), differing from that of the Coccidia in the thinness of its envelope, which permits it to absorb nutriment, like a gregarine. Over 500 oöcysts have been found by Grassi in the stomach-wall of a single *Anopheles* mosquito. As the oöcyst grows, its nucleus, at first single, divides to form a number of daughter nuclei, round each of which a small mass of protoplasm is centred (Fig. 68, XV, XVI). The segments thus formed have received various names, such as blastophores, zoidophores, or spore-mother-cells (Lankester), but they are evidently comparable to the sporoblasts of Coccidia and other Sporozoa, and may conveniently be designated as such. The sporoblasts of the malarial parasites are irregular in form and are not completely separated from one another, but remain in connection by protoplasmic bridges. After formation of the sporoblasts is complete a certain amount of residuary protoplasm is left over, containing the melanin-granules originally present in the gametocyte.

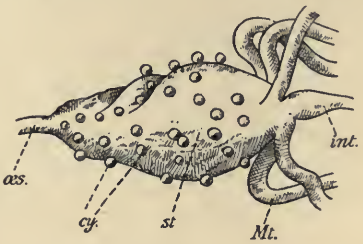

FIG. 71.

Stomach of a mosquito, with cysts of Haemosporidia. *oes*, oesophagus; *st*, stomach; *cy*, cysts; *Mt*, Malpighian tubules; *int*, intestine. (After Ross.)

In each sporoblast the single nucleus divides repeatedly to form a great number of small daughter nuclei, which travel to the periphery; the surface of the sporoblast then grows out into a number of slender protoplasmic processes, each of which takes one of the daughter nuclei with it (Fig. 68, XVII). In this way are formed a vast number of minute spindle-shaped sporozoites ("blasts," "zoids," "exotospores"), each about 14 $\mu$ long by 1 $\mu$

in breadth. The sporozoites are at first implanted upon the masses of residual protoplasm, representing the remnants of the sporoblasts, but soon free themselves and perform active movements within the cyst. The residual masses are usually enucleate, but sometimes contain residuary nuclei, which may even multiply, though doomed eventually to perish. Ultimately the residual masses derived from different sporoblasts appear to fuse into a smaller number of large granular masses, in which are found also the melanin-granules of the sporont (Fig. 68, XVIII). The whole number of sporozoites formed in this way in an oöcyst is very great, but varies within wide limits, from some hundreds to over ten thousand. The mosquito observed by Grassi, of which mention has been made above, might therefore have been capable of disseminating about five millions of malarial germs.

During the whole period of the development of the sporozoites, which lasts from ten to twelve days, the oöcyst grows continually in size. When the sporogony is complete the cyst bursts, and the sporozoites are set free in thousands in the body-cavity (haemocoele) of the mosquito. Here they are carried along in the circulating blood-fluid, and in some way are attracted towards the salivary glands, which they penetrate, filling the secreting cells. When a mosquito thus infected bites a man, it injects, in its usual fashion, a minute drop of saliva into the puncture made by its proboscis, and with the drop of saliva a swarm of sporozoites pass down into the blood, each the starting-point of a new infection and of many schizogonous generations. Thus the life-cycle of the parasite has been brought round again to the point which was selected for commencing the description.

From the above account it is seen that the life-cycle of the malarial parasite is now thoroughly known in all its features. There is, however, one point of importance still to be made out. In patients apparently cured of malaria it may appear again without a fresh infection, and it is not known what has been the condition of the parasite in the period intervening between the first attack and the relapse. In cases of chronic malarial cachexy, only crescents are to be found in the blood, and Grassi has suggested that the gametocytes may have the power of non-sexual reproduction in such cases, their offspring causing a reinfection of the host. This point has recently been investigated by Schaudinn [94*a*] in the case of the tertian parasite, and he finds that such cases of relapse are brought about by a sort of parthenogenetic reproduction on the part of the resistent, long-lived macrogametocytes. The nucleus of a macrogametocyte becomes slightly drawn out and shows at one extremity a number of deeply-staining, coarse grains of chromatin; it then divides into two, so that the gametocyte contains two nuclei, one rich in chromatin and staining deeply, the other pale and staining feebly. The body of the gametocyte may become partially constricted into two parts, one with denser protoplasm, with most of the pigment, and with the pale nucleus; the other with lighter protoplasm and less pigment, containing the dark nucleus, which now proceeds to divide as in schizogony and gives rise to a number of merozoites. The latter are the starting-point of fresh schizogonous cycles of generation, bringing about a return of the fever. The denser portion of the gametocyte with the pale nucleus is abandoned as residual protoplasm and breaks up. Only the female gametocytes are capable of reproducing themselves in this way. The microgametocytes, with their greatly enlarged nucleus and reduced bulk of protoplasm (see p. 248), are believed by Schaudinn to die off if they do not undergo their natural course of development in the intermediate host.

Attention must also be drawn to another point which is not yet fully explained. In mosquitos infected by these parasites, in addition to the ordinary cysts containing sporozoites, there occur also other cysts of about the same size, but very different in appearance, as they are filled with masses of dark brown pigment, which is quite different in appearance from the melanin-pigment of the parasites. Ross was the first to describe these bodies in *Culex* infected by *Haemoproteus danilewskyi* in birds, but they occur also in *Anopheles* infected with human malarial parasites. They have received various designations: "yellowish-brown bodies," Grassi; "black spores," Ross; "brown spores," Nuttall. Ross regarded them as resistent cysts, destined to develop in some unknown way, and Grassi at first thought they were intended to spread the infection amongst successive generations of mosquitos. It is, however, sufficiently well established that mosquitos neither come into the world infected with these parasites, nor acquire them in any other way but from the blood of their prey. Most authorities incline now to the later opinion of Grassi, and regard the yellowish-brown bodies as degenerate cysts of the ordinary kind, the pigment being produced by a protoplasmic mass consisting partly of the residual substance, partly of abortive sporozoites left behind in the cyst. This conclusion receives indirect support from the observations of Schaudinn [51*a*] upon the degenerated ŏöcysts of *Cyclospora* (see p. 273).

In the above description of the life-cycle, the mosquito has been referred to as the "intermediate host." Many authorities, however, such as Grassi, Mesnil, Laveran, and others of great note, consider that the Invertebrate host, the mosquito, should be regarded as the "principal" or "definitive" host, and the Vertebrate, man, as intermediate, chiefly on the ground that the sexual phases of the parasite are passed through in the former. In considering these conceptions, it should be made clear at the outset in what sense the term "principal host" is used. If it be employed in the sense of the primary or primitive host, then it must certainly be applied to the Vertebrate, for, while all the Haemosporidia have a Vertebrate host, there is at present no evidence whatever, in the case of many of them, that an Invertebrate host has been acquired as a means of dispersal (see below, p. 263). The Haemosporidia as a whole must be considered as parasites of Vertebrates in the first instance, which have in some cases adapted themselves for certain phases of their life-history to a secondary Invertebrate host. If, on the other hand, the term "principal host" be employed in a physiological or functional sense, it is again the Vertebrate that must be so distinguished. The essence of being a parasite is not to reproduce sexually, but to flourish at the expense of other creatures, and the term "host" denotes the being that suffers in proportion as the parasite profits. Of the two hosts of the malarial parasite there can be no question that in this sense also the Vertebrate is the principal one, since the mosquito appears to suffer scarcely at all. It certainly would not be in the interests of the parasite that the vitality of the mosquito should be lowered and its appetite impaired.

Those who term the Vertebrate the intermediate host of the malarial parasite, do so chiefly on the analogy of parasitic worms, Cestodes or Trematodes, in which the sexual stages are passed in the definitive host, the larval stages in an intermediate host. But the relation between schizont and sporont can scarcely be considered analogous to that between *Cercaria* and *Distomum*, for example. The comparison should be rather with the summer and winter generations of *Aphis* or *Daphnia*, or with Hydroid and Medusa.

The variations in the structure and life-history of other Haemosporidia, as compared with the type here selected, are best considered, as was done in Coccidia, first from the point of view of the morphology of the individual stages, secondly from that of the life-cycle considered as a whole.

(1) *Morphology.*—The trophozoites of Haemosporidia may be distinguished, speaking generally, either as "haemamoebae" or as "haemogregarines." Those parasitic upon cold-blooded Vertebrates are not amoeboid like the malarial parasites, but have a fixed body-form like minute gregarines (Figs. 75-77). This is true not only of the "free" phases, but also of the endoglobular forms. They occur generally as tiny vermicules, lodged in the blood-corpuscle or free in the blood-plasma. When free they are often very active in their movements, bending and twisting their bodies from side to side, or gliding forwards in the manner already described for Gregarines or Coccidian sporozoites (pp. 180 and 210), by the help of a secreted thread of gelatinous substance (Hintze [68]). The fixity of the body-contour seems to be due to the dense hyaline ectoplasm, in which myocyte-fibrillae can often be made out. The haemogregarines vary greatly in size, in different genera, relatively to the dimensions of the blood-corpuscles they attack. Thus, while *Lankesterella* scarcely attains to half the length of the frog's blood-corpuscle which it inhabits (Fig. 75), the species of *Haemogregarina* parasitic in various reptiles grow to such a length that in later stages the trophozoite becomes folded on itself in a characteristic manner, in order to be packed away within the limited space at its disposal (Fig. 77). The genus *Piroplasma*, on the other hand, is characterised by pear-shaped trophozoites of extremely small size, several of which may be lodged in a single blood-corpuscle (Fig. 80).

The reproductive phases of the majority of Haemosporidia are very imperfectly known, and in most cases the statements that have been made require revision, or at all events reinterpretation, in the light of recent discoveries. As regards the non-sexual cycle, it is interesting to note that in many forms the schizogony takes the most primitive form of multiplication by simple binary fission. This is the case in the species of the genus *Piroplasma*, where the pear-shaped trophozoite divides within the blood-corpuscle into two twin bodies, from which circumstance the type-species of the genus has received the specific designation *bigeminum*. Each of the daughter trophozoites may in its turn divide again. A similar binary fission occurs also in the species *Haemogregarina bigemina*, recently discovered by Laveran and Mesnil [79] in two species of blennies. In the majority of Haemosporidia, however, the schizont divides up simultaneously into a number of merozoites, which may be disposed in various ways. Besides the "rosette" or "daisy" pattern described above for *Laverania*, they may be arranged in the form of a "barrel," with the residual protoplasm at one extremity, as in the Eimerian phases of Coccidia, or they may be implanted on each side of the residuum, or in other ways. Sometimes the arrangement may vary in the same species, as in *Lankesterella* (*Drepanidium*) *ranarum*, where the merozoites may be formed on one side only of the schizont, or may have the radiate, daisy-like arrangement. The schizogony is usually intracellular, and takes place within a blood-corpuscle, or in the cells of certain internal organs, more particularly the spleen, liver, and bone marrow. The schizont often becomes surrounded by a membrane, forming a so-called *cytocyst* (Fig. 73). Sometimes, however, the sporulation may be free, *i.e.* extracellular, especially in the spleen-pulp.

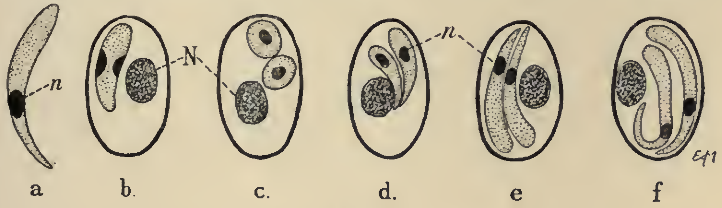

FIG. 72.

*Haemogregarina bigemina*, Laveran, from the blood of blennies. *a*, the form of the parasite found free in the blood-plasma. *b*, parasite within a blood-corpuscle, preparing for division; the nucleus has already divided. *c*, the parasite has divided into two rounded corpuscles, which assume the form of the free parasite, as seen in *d*, *e*, and *f*. *N*, nucleus of the blood-corpuscle; *n*, nucleus of the parasite. The outline of the blood-corpuscle is indicated by a thick black line. (After Laveran.) Magnified about 1800 diameters.

In many Haemosporidia of cold-blooded animals there appears to be a well-marked dimorphism in the schizonts, as well as in the merozoites produced by schizogony. Within the cytocyst the schizont may break up into smaller micromerozoites or larger macromerozoites.[1] This occurs in the form *Karyolysus lacertarum* (Fig. 73), and also in the haemogregarines infesting various snakes studied by Lutz [82] and named by him "*Drepanidium serpentium.*" In the latter the two kinds of merozoites develop into two forms of schizonts termed by Lutz microhaemozoites and macrohaemozoites respectively. Dimorphism in the cytocysts has also been described by Labbé in *Lankesterella*, but has not been confirmed by recent observers. The most obvious interpretation of these facts would seem to be that in these forms the schizonts show a precocious sexual differentiation comparable to what is seen in *Adelea* amongst Coccidia.

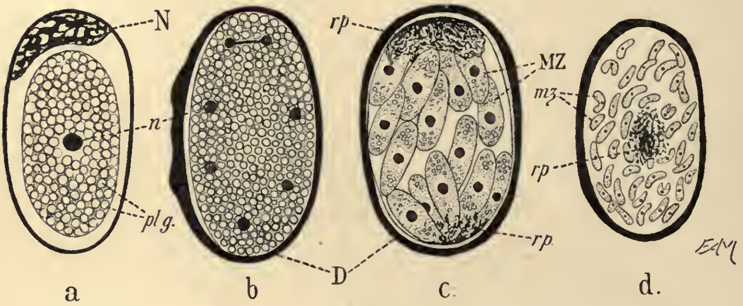

Fig. 73.

*Karyolysus lacertarum*, Labbé, sporulation. *a*, macroschizont crammed with plastinoid granules (*pl.g*) encysted in a blood-corpuscle, forming a cytocyst. *b*, later stage of the same; the schizont has grown in size, its nuclei (*n*) are multiplying, and the degenerated remains of the corpuscle and its nucleus (*D*) form the outer envelope of the cytocyst. *c*, cytocyst containing macromerozoites (*MZ*) and two residual masses of protoplasm (*r.p*), one at each pole. The macromerozoites, distinguished by their large size, contain a few small plastinoid granules. *d*, cytocyst containing micromerozoites (*mz*) and a single residual mass (*r.p*). *N*, nucleus of the blood-corpuscle; *n*, nucleus of the parasite. (After Labbé.) × about 1600 diameters.

Observations upon the sexual cycles of Haemosporidia are as yet few and somewhat far between, and it is necessary to be very cautious in making generalisations. The parasites of birds and man have been the chief objects of research, but not much is known with regard to the Haemosporidia of the lower Vertebrata. Recently, however, Hintze [68] has brought forward interesting observations upon *Lankesterella ranarum*. The microgametocytes (Fig. 75, *g*) are distinguished by their slender form, and by the absence of all but the finest granulations in their protoplasm, from the plump, coarsely granular macrogametocytes (Fig. 75, *j*), the ordinary schizonts being intermediate in character between the two. In the microgametocytes the nucleus contains a number of chromatin granules, each of which divides into two. The nucleus then becomes fragmented, and the chromatin-granules, each still half the size of those originally present, scatter themselves in the cell and become the nuclei of microgametes, which are not separated off simultaneously, but one by one, in an irregular manner (Fig. 75, *h*, *i*). In the macrogametocytes the entire nucleus divides into two, and one half degenerates, the other half becoming the pronucleus of the macrogamete (Fig. 75, *k*, *l*). In *Haemoproteus* ( = *Proteosoma*), however, the maturation of the macrogamete takes place, according to Schaudinn [93], by extrusion of the karyosome, as in *Coccidium*.

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[1] Commonly, but probably wrongly, termed microsporozoites and macrosporozoites.

It is common for the male and female gametocytes to be distinguishable from one another by well-marked characters. The microgametocytes have finely-granulated, hyaline protoplasm, while that of the macrogametocytes is more coarsely granulated, differences which have a considerable effect upon their staining properties in microscopic preparations. On the other hand, the grains of melanin-pigment are generally larger and more numerous in the microgametocytes. In *Halteridium* the form of the nucleus differs in the two sexes of the gametocyte (Fig. 79), and there is consequently also a difference in the arrangement of the melanin-granules, which in the male elements are placed at the two poles of the body, but in the female gametocytes are evenly scattered in the protoplasm.

The microgametes in all known cases are without any true flagella, like those of *Benedenia* and *Adelea* amongst Coccidia, but while in the human parasites and in the allied genera from birds they are long, slender, and flagelliform, in *Lankesterella* they are described as minute oval bodies, capable of amoeboid movement. The formation of the male gametes, the so-called "flagella," is a very striking and characteristic phenomenon, easily observed in the Haemosporidia of warm-blooded vertebrates, and described in many forms since it was first seen by Laveran. Macallum [83] gives the following graphic description of the process :—

"The adult organism is seen to draw itself together into a sphere within the red corpuscle, and sometimes immediately, but more often after a short delay, it begins to be greatly agitated, the pigment dancing about, and the surface of the sphere taking on an active undulating motion, which lasts but a short time, for the organism suddenly bursts from the corpuscle, scattering the remains of the latter, and in its place beside the nucleus of the corpuscle, which now lies free in the plasma, it throws out four or more flagella, which thrash about wildly, and sooner or later become detached and wriggle away. The sphere is much reduced in size by this throwing out of flagella, and the pigment is concentrated. . . . The remains of the sphere continue to be agitated, and after the loss of the flagella, its pigment sets up a most active dancing. Often it constricts itself into two or more parts, which may reunite. . . . Disintegration and death are the inevitable fate of these remains of the flagellated body, even if it escapes for

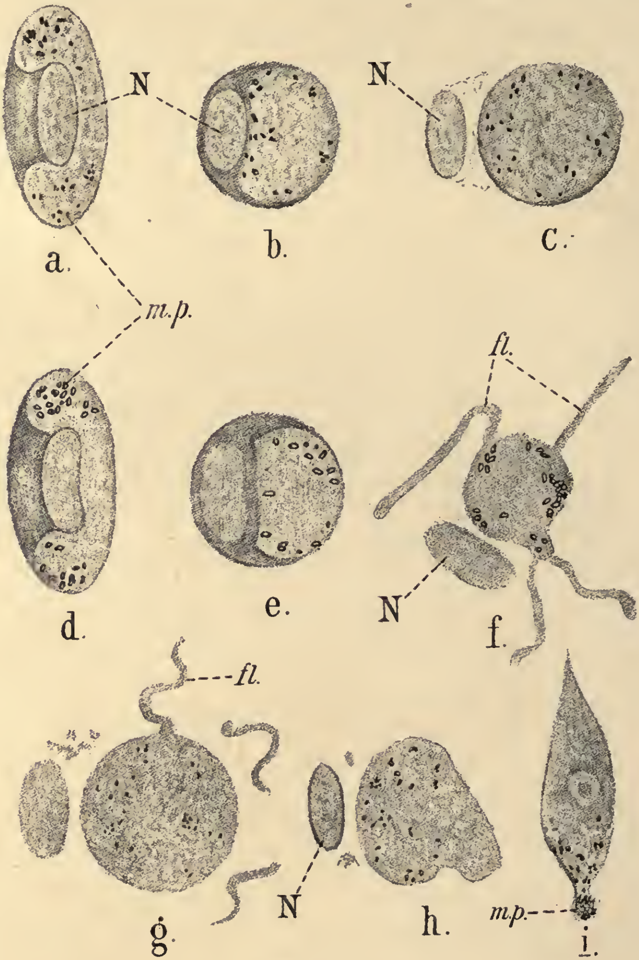

FIG. 74.

Formation of gametes, and fertilisation, in *Halteridium* (par. birds), after Macallum. *a*, female gametocyte in a blood-corpuscle. *b*, the same assuming the spherical form. *c*, the same in the spherical condition and freed from the disintegrated blood-corpuscle. *d*, mature male gametocyte in a blood-corpuscle. *e*, the same assuming the spherical form. *f*, the same freed from the corpuscle, throwing out "flagella" or male gametes. *g*, male gametes swarming round a female, which one of them (*fl*) is actually penetrating. *h*, the zygote throwing out a protoplasmic process on one side (the right). *i*, the zygote transformed from an inactive sphere into a motile "vermicule," moving forwards, with the melanin-pigment gathered at the posterior extremity. *N*, nucleus of the blood-corpuscle; *m.p*, melanin-pigment; *fl*, male gametes.

any length of time one of the voracious leucocytes which wander about."

The conjugation was first observed by Macallum in the genus *Halteridium* from birds, and his discovery gave the first clue to the nature of the "flagella," and showed that the "Polymitus" form belonged to the normal cycle of the parasite, in contradiction to the views then prevailing amongst most authorities upon the Haemosporidia, who regarded this phase of the parasite as a process of degeneration. The following is the account of the process of conjugation, and the subsequent formation of the motile zygote, given by Macallum, whose figures are also reproduced here (Fig. 74):—"The two forms [*i.e.* a granular macrogametocyte and a hyaline microgametocyte] lay at some distance from one another [on the field of the microscope]. . . . The granular form happened to escape from the corpuscle first, and lay perfectly quiet beside the free nucleus and the shadow of the corpuscle. Soon the hyaline body, becoming greatly agitated, burst from the corpuscle and threw out active flagella, which beat about for a few minutes and finally tore themselves loose. . . . One of the four flagella passed out of the field, but the remaining three proceeded directly towards the granular form, lying quietly across the field, and surrounded it, wriggling about actively. *One of the flagella, concentrating its protoplasm at one end, dashed into the granular sphere, which seemed to put out a process to meet it, and buried its head, finally wriggling its whole body into the organism, which again became perfectly round.* The remaining flagella, seeking to repeat this process, were evidently repulsed, and soon became inactive and degenerated. Immediately on the entrance of the flagellum, the pigment of the organism was violently agitated, without, however, any disturbance of the outline of the organism. Soon all became quiet again, and the period of quiescence lasted about fifteen minutes, when a conical process began to appear at one margin of the organism, which, increasing in size, drew into itself most of the protoplasm, the pigment, to a certain extent, being gathered in the remainder. Finally, most of the pigment was concentrated into a small round appendage, which remained attached to what now had become an elongated fusiform body [the oökinete or vermicule], which soon swam away with a gliding motion."

The fertilisation has been studied also by Schaudinn in *Haemoproteus* and in the tertian parasite, and by Hintze in *Lankesterella.* In the two former a cone of reception is formed by the macrogamete, but in the latter a fine canal is formed, along which the male pronucleus is guided from the point of entry up to the female pronucleus. The zygote resulting from fertilisation is in all cases, apparently, at first a freely-moving gregarine-like vermicule or "oökinete," which seeks out actively, and penetrates, the cells or

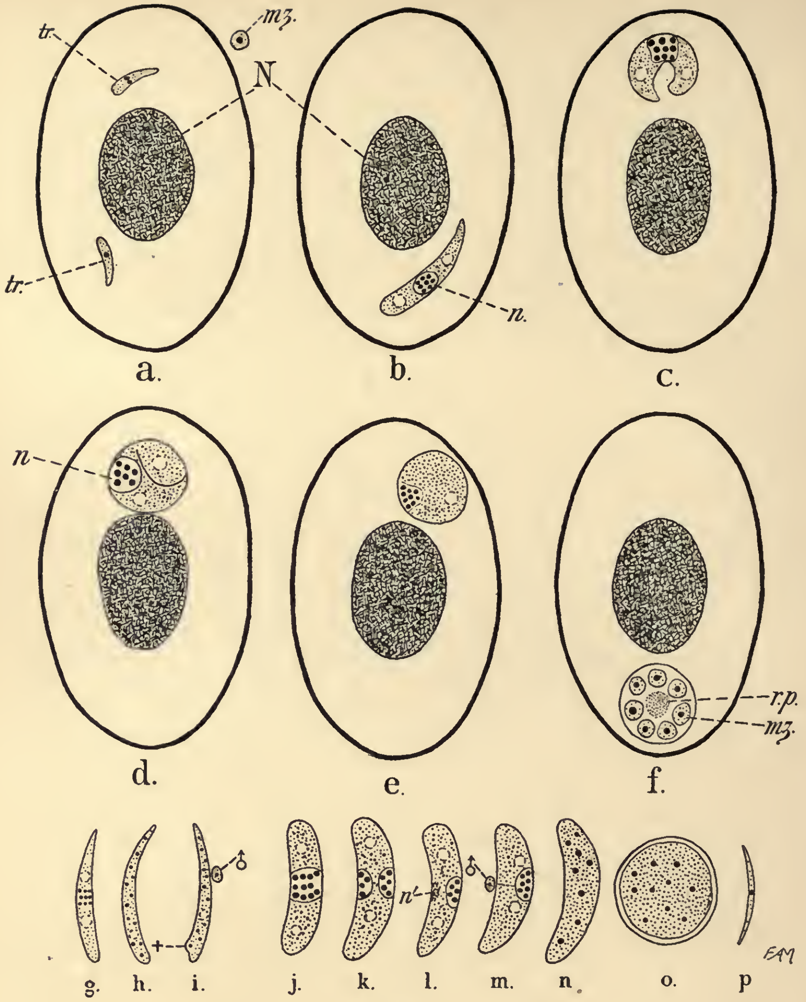

Fig. 75.

*Lankesterella ranarum* (Lank.) (par. *Rana esculenta*), phases of the life-history. *a-f*, schizogony. *a*, youngest stages of the parasite; *mz* shows a free merozoite; *tr*, *tr*, two young trophozoites within a blood-corpuscle, with one and two chromatin bodies respectively. *b*, a blood-corpuscle, containing a full-grown trophozoite (schizont), with numerous chromatin bodies, preparing to sporulate. *c*, the schizont is taking the form of an U. *d*, The schizont has become spherical, but still shows the line of suture between the two loops of the U in the last stage. *e*, the schizont is a perfect sphere. *f*, the schizont is segmented up into a number of merozoites (*mz*) round a mass of residual protoplasm (*r.p*). *g-i*, formation of microgametes. *g*, a full-grown microgametocyte with minute chromatin corpuscles in the nucleus. *h*, the chromatin corpuscles are dispersed through the body. *i*, a microgamete (♂ *g.*) is separated off, and another is forming at +. *j-m*, maturation of the macrogamete. *j*, full-grown macrogametocyte. *k*, the nucleus of the macrogamete has undergone division into two. *l*, one of the nuclei (*n'*) is degenerating. *m*, at the spot where the nucleus of the macrogamete underwent degeneration, a microgamete (♂) has attached itself, and from this spot a fine canal leads to the nucleus of the macrogamete. *n-p*, sporogony. *n*, a zygote, still motile, with fragmented nucleus. *o*, an encysted zygote, or oöcyst. *p*, a sporozoite. *g-i* and *n* are free in the blood-plasma. *j-m* are in blood-corpuscles in the same way as *a-f*. *o* is encysted in an epithelial cell of the intestine. *N*, nucleus of the blood-corpuscle; *n*, of the parasite. (After Hintze.) Magnified 2250 diameters.

tissues in which it comes to rest and becomes encysted as an oöcyst. In all cases that have been recently studied, the oöcyst is formed in the epithelium of the digestive tract, either of the same or of an intermediate host.

With regard to the sporogony, two types can be recognised, the differences between which depend upon whether the oöcyst is actively parasitic upon the tissues in which it encysts, as in the malarial parasites, or whether it forms round itself a tough protecting membrane within which it is more or less independent of its host or of external conditions, as in *Lankesterella* (Fig. 75, *o*). The latter case is undoubtedly the more primitive, and does not differ essentially from the state of things seen in the Coccidia. In the oöcyst of *Lankesterella* the number of sporoblasts is relatively small, and each sporoblast appears to give rise to a single sporozoite only. This condition is related, in this instance at least, with absence of an intermediate host. Sporogony and schizogony here go on in the same animal. On the other hand, in the malarial parasites of birds and man, perhaps of all warm-blooded animals, sporogony takes place, as in *Laverania*, in an intermediate host, upon which the oöcyst is actively parasitic. The enveloping membrane in these forms is very thin—according to Grassi it is formed by the host and not by the parasite—and the zygote grows greatly in size, forms a number of sporoblasts, and each sporoblast gives rise to very numerous sporozoites, as described above for *Laverania*. This great increase of reproductive power must be regarded as a secondary adaptation of a kind common in all forms of parasitic organisms, whereby the chances of disseminating the parasite amongst fresh hosts are much heightened by the vast number of germs produced from each individual.

In no case, however, are sporocysts secreted within the oöcyst. The sporozoites whether few or numerous, are naked gymnospores, similar to those of the genus *Eimeria* amongst Coccidia.

The Haemosporidia have been the object of extended studies on the part of Labbé, many of whose statements, however, still require confirmation, especially with regard to the forms inhabiting cold-blooded vertebrates, *i.e.* the genera *Lankesterella*, *Karyolysus*, and *Haemogregarina*. It is asserted by him, with regard to the first two genera, that a trophozoite, after growing to a certain size within a blood-corpuscle, becomes free in the blood-serum, and that an isogamic conjugation takes place between two perfectly similar free individuals; and that then the zygote so formed penetrates a second blood-corpuscle, or it may be a cell of the spleen, liver, kidney, or bone-marrow, and forms a resistent cyst within which it breaks up into sporozoites. A certain amount of scepticism has grown up with regard to these statements, which are not in any way confirmed by the recent observations of Hintze upon *Lankesterella*, and receive no support from the analogy of what is known in other forms.

(2) *Life-history.*—It is probable that an alternation of generations, of schizogony and sporogony, occurs in all Haemosporidia, and that there are no forms in which the schizogony is non-existent or suppressed, as in *Benedenia* amongst Coccidia; though there are many in which the sporogony has not yet been described. The most salient feature in which the life-cycles of different forms differ from one another is the mode of infection; that is to say, with regard to the presence or absence of an intermediate host, in which the sporogony takes place, and which serves to disseminate the parasite. The brilliant investigations of Ross upon the Haemosporidia of birds first demonstrated the agency of blood-sucking gnats of the genus *Culex* in spreading the infection amongst avian hosts, and the organised researches of Grassi and his Italian fellow-workers have proved incontestably the part played by other mosquitos of the genus *Anopheles* in carrying involuntarily the malarial germs from one human being to another. In a similar way it has been proved experimentally that the parasite of the Texas cattle-fever, *Piroplasma bigeminum*, is transmitted from one ox to another by ticks (*Rhipicephalus annulatus* = *Boophilus bovis*); but in this case the part played by the intermediate (invertebrate) host is much more complicated than in the infection of birds or man with malaria by gnats, since the parasite passes through two generations of ticks.

The ticks which nourish themselves upon cattle and other mammals become sexually mature at their last moult. They then pair, and the fertilised females, after gorging themselves with blood, drop off on to the ground. Each female then lays about 2000 eggs, and within the shell of each egg a large quantity of blood is deposited, to serve as vitellus for the developing embryo. When oviposition is completed, the female shrivels up, and becomes a dried, empty, lifeless skin. From the egg is hatched a larva, which has only three pairs of legs, and contains in its abdomen a certain quantity of blood, the still unabsorbed remains of its share of its mother's last meal. The newly-hatched larva crawls on to a blade of grass or other convenient coign of vantage, from which it either passes on to the skin of a fresh host, or drops off dead from starvation, if no favourable opportunity occurs for changing its situation before its supply of blood is exhausted.

A remarkable fact, with reference to the transmission of Texas-fever, was first demonstrated experimentally by Smith and Kilborne, and subsequently confirmed by Koch [70] and other observers, namely, that if the mother-tick drew its supply of blood from an ox infected with *Piroplasma*, *her progeny are born into the world infected with the parasite*, and become the means of disseminating the disease amongst healthy cattle. Thus is explained the long incubation-period of the disease, the time required for it to spread from diseased to healthy cattle being about forty-five to sixty days; of this thirty days are taken up by the development of the egg of the tick, the remainder probably by the development of the parasite within the ox (Smith [97]).

From the facts it would appear at first sight as if the infection of the young ticks was a case of true hereditary infection, parallel to the "pébrine" disease of the silkworm. But it is quite possible that the tick-embryo acquires the infection secondarily from the blood it absorbs in the egg, and it does not follow that the parasitic germs pass through the ovum itself as in *Glugea*. Until something is known of the stages of the parasite within the tick, it is not possible to decide whether this is a case of true hereditary infection or not.

The number of instances in which intermediate hosts have been demonstrated for Haemosporidia has been increased so steadily by recent researches that many authorities are inclined to the belief, to which expression has recently been given by Börner, that for all species of Haemosporidia there is some blood-sucking animal which is the agent in the dissemination of the parasites, and that where no intermediate host is known, it merely remains to be discovered.

There are, however, many grounds against believing that an intermediate host occurs in all cases. First, on general grounds, if the modern conception of the Haemosporidia as forms closely allied to Coccidia, adapted to parasitism upon blood-cells, be correct, it is reasonable to suppose that the ancestors, at least, of the group under consideration were at first without any special means of dissemination other than the resistent spores and cysts found in Coccidia and Sporozoa generally; and if this be admitted, it becomes further highly probable that representatives of these primitive forms will be found to exist at the present day. Secondly, empirical grounds are not wanting to support these conclusions, although decisive experimental proof is lacking as yet. In a great many instances amongst the Haemosporidia of the lower Vertebrata, sporogony as well as schizogony occurs in the Vertebrate host. In the case of the *Lankesterella* of the frog, Hintze has shown that the motile zygote leaves the blood to encyst in an epithelial cell of the gut, and that the resistent cyst so formed passes out with the faeces. We find here, therefore, just those conditions for disseminating the parasites which are most typical of Sporozoa generally. It is highly probable that the infection of the frog by *Lankesterella* is a casual one, brought about by the frog swallowing cysts of the parasite accidentally, and this conclusion is supported by the fact that, according to Hintze's observations, frogs living in pools and confined spaces are especially liable to the infection, while those from rivers and large areas of water are almost entirely free from it.[1]

There is therefore a very strong case in favour of the view expressed by Schaudinn, namely, that many Haemosporidia, especially those of cold-blooded Vertebrata, are not disseminated by an intermediate host, but that the infection is a casual one, as in any other kind of Sporozoa. It is evident that the acquisition of an intermediate host is an adaptation which is vastly beneficial from the point of view of the parasite, as is shown by the rapidity with which the diseases caused by them spread in countries where the two necessary conditions occur—the presence, that is to say, both of the parasite and of its blood-sucking intermediate host. The latter in all cases hitherto investigated has turned out to be an Arthropod, within which the sporogony of the parasite takes place, and upon which the oöcysts are actively parasitic. A general survey of the life-cycles of Haemosporidia and Coccidia would lead one, however, to believe that primitively the sporulating stages would not have been parasitic upon the intermediate host, but that the latter would have acted merely as a carrier and not as a host, in the strict sense of the word. A life-cycle of this kind remains as yet hypothetical, but may be postulated as a stage in the evolution of the adaptive relation between parasite and blood-sucker, even if non-existent at the present day.

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[1] Compare the very similar case of *Lithobius* from different localities as regards infection with *Coccidium*, above, p. 221.

(*c*) *Classification.*—The nomenclature and taxonomy of the Haemosporidia is in a very confused state. It is not uncommon to find the same form appearing in the literature under three or more different names, or to see the same name applied to designate totally distinct objects. Of recent years, however, much has been done to introduce order into this chaos, and students of the group are slowly but surely coming to an agreement as to the correct names of the different forms of Haemosporidia, in accordance with settled zoological usage. There is still, however, considerable diversity of opinion as to the manner in which the parasites should be grouped together.

Labbé [4] classifies the Haemosporidia, as here understood, under two orders, the Haemosporidia *sensu stricto*, and the Gymnosporidia (= Acystosporidia of Wasielewski). The first of these divisions comprises the species parasitic for the most part upon cold-blooded animals, in which schizogony and sporogony occur in the same host. The Gymnosporidia, on the other hand, are the forms parasitic upon warm-blooded hosts, and owe their name to the fact that no resistent cysts are formed by them in the Vertebrate host, since the sporogony takes place, so far as has been observed, in an intermediate Invertebrate host. Recent authorities have for the most part abandoned this classification, but in so far as it separates the more primitive forms, without special intermediate hosts, from those in which an alternation of habitat has been evolved, it is probably a useful and, to a large extent, a natural mode of grouping these parasites. Labbé's two orders have therefore been revived by Neveu-Lemaire [88] as two sub-orders of the order Haemosporidia, and they are retained here in this sense, but with the terminations altered, in order to avoid confusion between the name of the order and that of the first of the two sub-orders.

The majority of writers upon the Haemosporidia are content simply to enumerate the various genera comprised in this order, without grouping them into families. Recently, however, Neveu-Lemaire has recognised four families, without defining them, to include a certain number, but not all, of the known genera of Haemosporidia. These are—(1) the family *Haemogregarinidae*, equivalent in extent to the whole sub-order Haemosporidia *sensu stricto*, and comprising the genera *Lankesterella* (=*Drepanidium*), *Karyolysus*, and *Haemogregarina*; (2) family *Haemamoebidae* (Wasielewski), comprising the genera *Plasmodium*, *Laverania*, and *Haemamoeba* (=*Haemoproteus* s. *Proteosoma*); (3) family *Halterididae* for *Halteridium* and *Polychromophilus*; (4) family *Achromaticidae* for *Achromaticus* and *Dactylosoma* (synonym of *Drepanidium*). Amongst the genera left out in the cold is *Piroplasma* (=*Apiosoma*), a genus which is sufficiently well characterised to be the type of another family; while on the other hand the position and importance of the genera *Polychromophilus* and *Achromaticus* must remain for the present doubtful. The arrangement of the genera in families seems, therefore, rather premature in the present state of knowledge.

With regard to number of generic types to be recognised amongst the Haemosporidia, the greatest diversity of opinion prevails. Laveran [75, 77], to whose authority, as the original discoverer of the malarial parasites, the greatest weight attaches, recognises but three genera: (1) *Haemamoeba* [including *Plasmodium*, *Laverania*, *Haemoproteus*, etc.]; (2) *Piroplasma;* and (3) *Haemogregarina* [including *Drepanidium* and *Karyolysus*]. This classification has at least the merit of simplicity, but in lumping the genera together to such an extent, Laveran is not followed by other writers, and his three genera are to be regarded rather as representing groups of the value of families in a natural system.

In the following systematic review, the genera best characterised and commonly recognised are given first, and then a certain number of doubtful forms are briefly mentioned.

## ORDER **Haemosporidia**, Danilewsky.

### SUB-ORDER I. HAEMOSPOREA.

Trophozoite typically a vermiform haemogregarine, endoglobular in early stages, free when full grown. Apparently no alternation of hosts; schizogony and sporogony in the same host, which is always a cold-blooded vertebrate, fish, amphibian, or reptile.

Genus 1. *Lankesterella*, Labbé, 1899 (for *Drepanidium*, Lankester, 1882), preoccupied. The haemogregarine is not more than three-fourths the length of the blood-corpuscle it inhabits. Type-species *L. ranarum*,[1] Lankester (Fig. 75), parasitic on *Rana esculenta; L. monilis* (Labbé), from the same host, is apparently a distinct species. *L. avium* (Labbé), from birds, is believed by Grassi to be the oökinete stage of *Halteridium danilewskyi*. Genus 2. *Karyolysus*, Labbé, 1894. The haemogregarine does not exceed the blood-corpuscle in length. One species, *K. lacertarum* (Danil.) (Figs. 73, 76), from lizards (*Lacerta* spp.). To this genus, probably, should be ascribed the parasite of *Testudo ibera* described by Popovici [91], and perhaps also the "*Drepanidium serpentium*" described by Lutz [82] from a number of species of snakes. Genus 3. *Haemogregarina*, Danilewsky, 1885 (syn. *Danilewskya*, Labbé, 1894). The body of the parasite exceeds

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[1] According to Hintze [68], this form was first described by Chaussat in 1850 under the name of *Anguillula minima*, so that its correct designation would be *Lankesterella minima* (Chaussat).

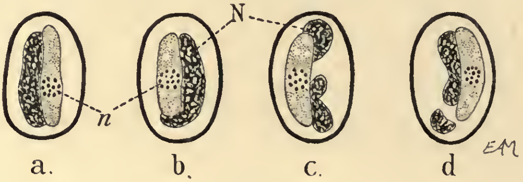

FIG. 76.

*Karyolysus lacertarum* (Danil.), in the blood-corpuscles of *Lacerta muralis*, showing the effects of the parasite upon the nucleus of the corpuscle. In *c* and *d* the nucleus is broken up. *N*, nucleus of the corpuscle; *n*, nucleus of the parasite, seen as a number of masses of chromatin, not enclosed by a distinct membrane. (After Marceau.)

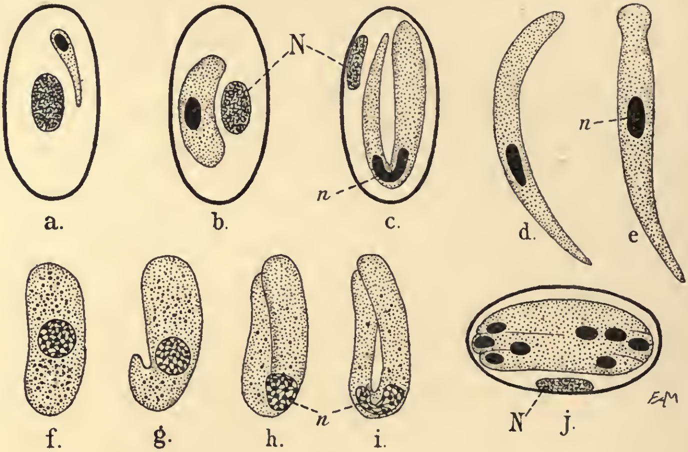

FIG. 77.

*Haemogregarina stepanovi*, Danilewsky (par. *Emys* and *Cistudo*), phases of the schizogony. *a*, blood-corpuscle with young trophozoite. *b*, older trophozoite. *c*, full-grown trophozoite, ready to leave the corpuscle. *d* and *e*, trophozoites free in the blood-plasma, showing changes of form. *f-i*, trophozoites still within the blood-corpuscle to show the structure of the nucleus, the coarse chromatoid granules in the protoplasm, and the manner in which the parasite grows into the U-shaped haemogregarine without increase of body-mass. *j*, commencement of sporulation; the nucleus has divided into eight nuclei, and the body of the parasite is beginning to divide up into as many merozoites within a blood-corpuscle. *N*, nucleus of the blood-corpuscle; *n*, nucleus of the parasite. (*a-e* and *j* after Laveran; *f-i* after Börner.) × 1000-1200 diameters.

the blood-corpuscle in length when adult, and is bent on itself within it in a characteristic manner, like the letter U. A large number of species from reptiles (Chelonia, Lacertilia, Ophidia, Crocodilia), of which the commonest are *H. lacazei* (Labbé), from *Lacerta agilis*, and *H. stepanovi*, Danil. (Fig. 77), from *Emys lutaria* and *Cistudo europaea*. *H. magna* (Gr. et Fel.), occurring in the frog, *Rana esculenta*, is perhaps the macrogamete of *Lankesterella ranarum* or *L. monilis*. Three species have recently been described from fishes: *H. delagei*, Lav. et Mesn., from *Raia punctata* and *R. mosaica*, *H. simondi*, Lav. et Mesn., from the sole, and *H. bigemina*, Lav. et Mesn. (Fig. 72), from two species of blennies. A doubtful species has even been described by Eisen under the name *H. nasuta*, from the blood of an Annelid (*Eclipidrilus frigidus*).

### SUB-ORDER II. ACYSTOSPOREA.

The trophozoite is an amoeboid haemamoeba, or is of simple body-form, and is typically endoglobular throughout the schizogonous cycle. An alternation of hosts is known in many instances to occur; the schizogony takes place in the vertebrate host, usually a warm-blooded animal (bird or mammal); the sporogony takes its course in an invertebrate host, which is an arthropod in all cases hitherto observed.

Genus 4. *Plasmodium*, Marchiafava et Celli, 1885 (syn. *Haemamoeba* auct.). The haemamoebae contain granules of melanin-pigment. The merozoites are oval in form, arranged in a single group round a central residual body. Gametocytes spherical. Two species generally recognised, both parasitic upon man; see above, p. 243. To this genus also Lühe refers the form discovered by Kossel in apes, and named by Laveran *Haemamoeba kochi*.[1] Genus 5. *Laverania*, Gr. et Fel., 1890 (syn. *Haemomenas*, Ross, 1899). Trophozoites and merozoites as in the last. Gametocytes crescent-shaped. One species, *L. malariae*, Gr. et Fel. (syn. *Haemamoeba* s. *Haemomenas* s. *Plasmodium praecox*, etc.), parasitic in human blood; see above, p. 243 (Fig. 68). Genus 6. *Haemoproteus*, Kruse, 1890 (syn. *Proteosoma*, Labbé, 1893). Trophozoites and merozoites as in the preceding. Gametocytes bean-shaped.[1] One species, *H. danilewskyi*, Kruse (syn. *Proteosoma grassii*, Labbé), parasitic on a large number of common birds (Fig. 78). The intermediate host is a gnat of the genus *Culex*. Genus 7. *Halteridium*, Labbé, 1894. Trophozoites as in the

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[1] Schaudinn, in his monograph on the tertian parasite [94*a*], unites forms here placed under the three genera, *Plasmodium*, *Laverania*, and *Haemoproteus*, in one genus, to which he gives the first of these three names; since he does not consider the differences in the form of the gametocytes to be an adequate generic distinction. The genus *Plasmodium* in his revision contains the following species:—

(1) *P. malariae* (Lav.), quartan parasite of man.
(2) *P. vivax* (Gr. et Fel.), tertian parasite of man.
(3) *P. immaculatum* (Gr. et Fel.), parasite of human pernicious malaria.
(4) *P. praecox* (Gr. et Fel.), the "Proteosoma" parasite of birds.
(5) *P. kochi* (Lav.), from the blood of apes.

The genus *Halteridium* Schaudinn considers to be distinct, but he declares that it should be named *Haemoproteus*, so that the halter-shaped parasite of birds stands as *Haemoproteus danilewskyi* (Gr. et Fel.)!

The confusion in the scientific names of these parasites is now so great as to lead to the remarkable result that the popular names commonly given to them furnish more distinctive and intelligible appellations than the ever-changing "correct" taxonomic nomenclature."

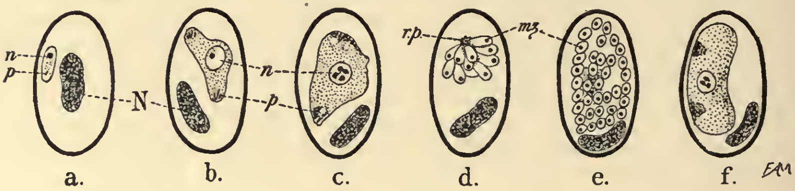

FIG. 78.

*Haemoproteus danilewskyi*, Kruse (par. birds). *a*, young trophozoite in a blood-corpuscle. *b* and *c*, older trophozoite. *d* and *e*, sporulation. *d*, precocious sporulation, with few merozoites. *e*, sporulation of a full-grown schizont, with numerous merozoites. *f*, gametocyte. *N*, nucleus of blood-corpuscle; *n*, nucleus of parasite; *p*, pigment; *mz*, merozoites; *r.p*, residual protoplasm. (After Labbé.) × about 1200. [*a*, *b*, *c*, and *f* from the chaffinch; *d* and *e* from the lark.]

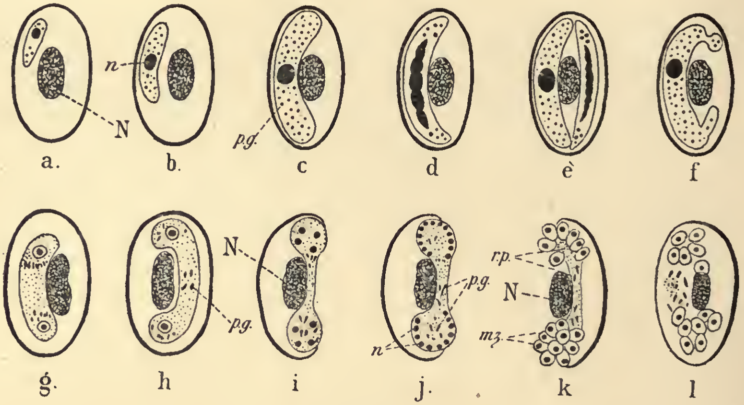

FIG. 79.

*Halteridium danilewskyi* (Gr. et. Fel.) (par. birds), various stages. *a*, young trophozoite in a blood-corpuscle. *b*, older trophozoite. *c*, macrogametocyte with spherical nucleus and evenly-scattered pigment-granules. *d*, microgametocyte, with elongated irregular nucleus and pigment-granules at the two extremities of the body. *e*, double infection, micro- and macro-gametocyte in the same corpuscle. *f*, macrogametocyte throwing out pseudopodia. *g-l*, schizogony. *g*, early stage of schizogony; the nucleus of the schizont has divided into two nuclei which travel to the two extremities of the body. *h*, the same stage more advanced. *i*, each of the two nuclei of the preceding stage has divided into four. *j*, the nuclei at the two poles have become very numerous. *k*, separation of merozoites (*mz*) and residual protoplasm (*r.p*) containing the pigment-granules; at one pole the arrangement of the merozoites is roughly fan-like, at the other, mulberry-like. *l*, commencing liberation of the merozoites. In the final stages of schizogony (*i-l*) the blood-corpuscle is acted upon and more or less broken up by the parasite. *N*, nucleus of blood-corpuscle; *n*, nucleus of parasite; *p.g*, pigment granules. (*a-f* after Laveran; *g-l* after Labbé.) × about 1200. [*a-f* from the pigeon; *g-j* and *l* from the lark; *k* from the chaffinch.]

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[1] According to Neveu-Lemaire, the name *Haemamoeba*, Gr. et Fel., 1890, has the priority over *Haemoproteus* for this genus; but the case does not seem very clear, and since the name *Haemamoeba* has many applications, and is often employed in a general as well as in a taxonomic sense, confusion is avoided by keeping to Kruse's name.

preceding; merozoites disposed in two groups, connected by the residual body. Gametocytes bean-shaped. One species, *H. danilewskyi* (Gr. et Fel.), parasitic upon various common birds (Fig. 79). Intermediate host not known. [The two forms of endoglobular parasites found in the blood of birds, *Haemoproteus* and *Halteridium*, are easily distinguished in all but the very youngest stages. *Haemoproteus* has an irregular, more or less compact form, occupies the centre of the corpuscle, and pushes the nucleus to one side, often compressing or deforming it (Fig. 78); sporulation takes place in the peripheral circulation. *Halteridium*, on the other hand, grows in a characteristic manner so as to resemble a halter in form, surrounding the nucleus, which is scarcely or not at all displaced (Fig. 79); it sporulates only in the internal organs, especially in the spleen and the bone-marrow.] Genus 8. *Piroplasma*, Patton, 1895 [1] (synn. *Pyrosoma*, Smith et Kilborne, 1893; *Apiosoma*, Wandolleck, 1895; *Babesia*, Starcovici, 1893). Trophozoites amoeboid, ovoid, or pear-shaped; schizogony by simple fission. Sexual cycle and sporogony unknown. Type-species *P. bigeminum* (Sm. et K.), parasite of Texas cattle-fever (Fig. 80); the disease is known to be transmitted by the bites of ticks (see above), but the phases of the parasite in the intermediate host have not been studied. Hunt [69] has found crescents in the blood of cattle, and has observed their change into a spheroidal shape, but while comparing these bodies to the crescents of the malarial parasites, he at the same time regards them as a form of sporulating body producing

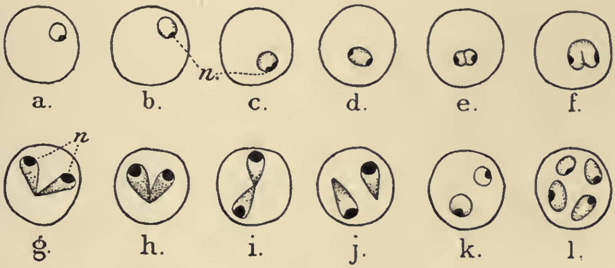

FIG. 80.

Development and schizogony of *Piroplasma bigeminum* in the blood-corpuscle of the ox. *a*, youngest form. *b*, slightly older. *c* and *d*, division of the nucleus. *e* and *f*, division of the body of the parasite. *g*, *h*, *i*, *j*, various forms of the twin parasite. *k* and *l*, doubly-infected corpuscles. (After Laveran and Nicolle.)

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[1] The nomenclature of the parasite of Texas-fever and its congeners is in a very confused state. The generic name *Pyrosoma* given to it by Smith and Kilborne in 1893, being preoccupied for the well-known Ascidian genus, was altered to *Piroplasma* by Patton in 1895 (not 1885, as wrongly stated by Labbé [4]), and in the same year Wandolleck gave it the name *Apiosoma*, which, however, had previously been given by Blanchard in 1885 to a genus of Ciliata (for *Apiosoma piscicola*, ectoparasitic upon the skin of fishes). From these data, *Piroplasma* would appear to be the correct name; but in 1893 Starcovici gave the name *Babesia bovis* to the blood-parasite of cattle described by Babes (1888) under the name *Haematococcus bovis*, which according to Laveran is identical generically and specifically with the Texas-fever parasite. If that is the case, the correct name of the genus would be *Babesia*, and the species parasitic on oxen should be called *Babesia bovis* (Babes).

spores endogenously, having mistaken the coarse granules in them for minute spores. Doflein [2*a*], however, distinguishes minute individuals, reproducing by schizogony, from large pear-shaped forms, which he regards as gametocytes. The latter have been observed by Lignières [81*a*] to round themselves off, and even (as this author's observations are interpreted by Doflein) to throw out "flagella," *i.e.* microgametes. The relations of the various phases hitherto observed, and their true rôle in the life-cycle, is at present, as Doflein observes, purely conjectural. Other species are *P. canis*, Piana et Galli-Valerio ; *P. ovis* (Starcovici) ; and *P. equi*, Laveran. *P. canis* has also been proved to be disseminated by dog-ticks ; in South Africa by *Haemaphysalis leachi ;* in Europe, apparently by *Dermacentor reticulatus.* See Nocard and Motas [89].

The following genera are of uncertain value, and can only be accepted provisionally :—

*Polychromophilus*, Dionisi, 1900, for two species, *P. murinus*, from the blood of *Vespertilio murinus*, and *P. melanipherus*, from another bat, *Miniopterus schreibersii.* Intermediate host unknown. Trophozoites and merozoites as in *Plasmodium.*

*Achromaticus*, Dionisi, 1900, for *A. vesperuginis*, from the bats of the genus *Vesperugo.* Distinguished from the preceding only by the absence of melanin-pigment in the haemamoeba. Intermediate host unknown. Neveu-Lemaire refers to this genus the species *Haemamoeba subimmaculata*, Gr. et Fel., from certain birds, perhaps a variety of *Haemoproteus danilewskyi*, Kruse.

*Cytamoeba*, Labbé, 1894, for *C. bacterifera*, Labbé, from the blood of *Rana esculenta*, remarkable for containing commensal bacteria. Perhaps a pathological variation or deformation of *Lankesterella ranarum.*

*Dactylosoma*, Labbé, 1894, for *D. ranarum* (= *D. splendens*, Labbé = *Laverania ranarum*, Grassi), from the blood of *Rana esculenta*, is, according to Hintze, a variety of *Lankesterella ranarum.*

*Karyophagus*, Steinhaus, 1889 (syn. *Acystis*, Labbé, 1894), for three species parasitic upon the epithelium of the intestine in the salamander (*K. salamandrae*, Steinhaus), the newt (*K. tritonis*, Steinh.), and the frog (*K. ranarum*, Labbé). They are Eimerian phases of Coccidia (see p. 230).

*Haemapium*, Eisen, 1897, for *H. riedyi*, an endoglobular haemamoeba from the red blood-corpuscles of *Batrachoseps attenuatus* (Urodela).

Finally, there remains for mention a species of which the exact position is not yet clearly defined, and which has been described under the generic designation *Haemamoeba*, in the sense of Laveran (see above, p. 265), namely, *H. metchnikovi*, Simond, from *Trionyx indicus*, observed at Agra. It occurs as a minute pigmented endoglobular amoebula resembling the malarial parasites of birds and mammals. Its presence in a cold-blooded animal is therefore remarkable and quite exceptional. The amoebulae grow into reniform bodies of two kinds, one with fine, the other with coarse pigment-granules. In addition there is found in the blood of the same hosts a non-pigmented haemogregarine which Simond believes to be also a phase of this parasite. Further investigations of this interesting form are required, and Laveran admits it only with some reserve to rank in his genus *Haemamoeba.*

## Comparison of the Life-Cycles of the Telosporidia.

It is evident that the Haemosporidia resemble the Coccidia very closely in all essential points. Their life-cycle can be described in identical terms, and the points of difference are mainly adaptive. They might, in fact, be considered simply as Coccidia adapted to parasitism upon a special form of cell, the blood-corpuscle, as has been done by Mesnil (see p. 229, footnote). This point of view is not, however, strictly accurate, as the Haemosporidia exhibit certain features, not obviously correlated with their mode of life, which are not seen in Coccidia. Such are (1) the frequent occurrence of amoeboid phases in the growth of the trophozoites; (2) the free, extra-cellular gregarine-like forms characteristic of one sub-order; (3) the occurrence of schizogony by simple binary fission; and (4) the motile "vermicule" phase of the zygote. Some of the above characters, notably (1) and (3), are clearly of a primitive nature, and could easily be explained as an inheritance from an ancestor common to them and to the Coccidia.

The two orders Haemosporidia and Coccidia may therefore be regarded as two very closely allied groups of the Telosporidia, which have diverged from a common origin in two directions, in accordance with the difference in their habitat. Doflein has recently given expression to this view by placing the Coccidia and the Haemosporidia as two sub-orders of a single order, the Coccidiomorpha.

On the other hand, the exact homologies between the different stages of the life-cycles of the Gregarinida and Coccidiomorpha respectively are not so obvious, and require brief discussion. In both groups the life-cycle may be complicated by schizogony, but for purposes of detailed comparison it is necessary to eliminate all secondary or adaptive phases of development, and to select types in which the life-history runs the simplest course. In other words, the comparison must start from the consideration of a monogenetic type of development by sporogony, such as is found in the vast majority of Gregarines, and in *Benedenia* amongst Coccidia.

In a typical Gregarine such as *Monocystis*, or, better still, *Stylorhynchus*, the life-cycle may be formulated as follows:—

$$\left.\begin{array}{l}\text{Sporozoite}\rightarrow\text{♀ Gametocyte}\times n\,\text{♀ Gametes}\\ \text{Sporozoite}\rightarrow\text{♂ Gametocyte}\times n\,\text{♂ Gametes}\end{array}\right\}+=n\text{ Zygotes}\rightarrow n\text{ Sporoblasts}\rightarrow n\text{ Spores}\times mn\text{ Sporozoites.}$$

In a monogenetic Coccidian, the life-cycle may be expressed thus:

$$\left.\begin{array}{l}\text{Sporozoite}\rightarrow\text{♀ Gametocyte}\rightarrow\text{♀ Gamete}\\ \text{Sporozoite}\rightarrow\text{♂ Gametocyte}\times n\,\text{♂ Gametes}\end{array}\right\}+=\text{Zygote}\times n\text{ Sporoblasts}\rightarrow n\text{ Spores}\times mn\text{ Sporozoites.}$$

Comparing these two formulae,[1] it is seen that the main differences between the two types are seen in two points. First, the female gametocyte in Coccidia gives rise only to a single female gamete, instead of to a number of them, and consequently there is only a single zygote, and a certain number of male gametes are wasted; secondly, the zygote of the Gregarine becomes a sporoblast, and ultimately a spore, but the zygote of the Coccidian becomes the oöcyst, and gives rise to a number of sporoblasts, each of which becomes a spore.

The facts stated above have led some authors to abandon the obvious comparison of spore to spore and cyst to cyst in Gregarinida and Coccidiidea respectively. Taking the zygote as the fixed point, so to speak, in both types of development, it has been urged that the product of zygosis should be strictly homologised and that therefore the Coccidian oöcyst should be compared with the Gregarine sporocyst. From this basis of comparison the Coccidian sporocyst is something not represented in Gregarines, and similarly the Gregarine cyst is without parallel amongst Coccidia. This interpretation of the homologies seems to raise more difficulties than it solves, and we shall attempt to show that the facts can be interpreted differently, and in a manner at once simpler and more natural.

There is one point in which the two life-cycles differ, which is not shown by the formulae given above, but which is of crucial importance. In Gregarines the two sporonts become enveloped in a common cyst *before* they give rise to gametes, and the entire process of zygosis goes on within the cyst. In Coccidiomorpha the zygosis takes place between free gametes, which become encysted *after* the process is complete. The rare instances in which an oöcyst is secreted by the female gamete before fertilisation, as in *Coccidium proprium*, etc. (p. 227), is not really an exception to this rule, since here also the male gametes are free, and a micropyle is left for their entry into the oöcyst.

The relation of the encystment to the zygosis is probably the clue to the solution of the problem, and affords a means of tracing a simple phylogenetic origin for the two divergent types of life-history. As an ancestral condition, common to all Telosporidia, we may assume a type in which the gametocytes each formed a number of gametes, as in Gregarines, these gametes, however, being, like those of the Coccidia, free, that is to say, not enveloped in any cyst. The trophozoites of this ancestral form were probably entirely intracellular, and the gametes formed by them were probably differentiated into active male gametes and passive female gametes. Nevertheless, the male gametes must often have failed to find the female gametes, which would then have to develop parthenogenetically, or to perish unfertilised. From this hypothetical ancestral stage the state of things existing in both Gregarines and Coccidiomorpha may be derived by simple processes of adaptive improvement and specialisation.

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[1] The formulae of the life-cycles are simplified, but not modified for purposes of comparison, in those cases in which the sporoblasts are transformed into gymnospores or so-called sporozoites, as in *Aggregata* amongst Gregarinida and *Eimeria* (*Legerella*) amongst Coccidiidea. In such cases, instead of "$n$ Sporoblasts $\rightarrow n$ Spores $\times\, mn$ Sporozoites," we must write "$n$ Sporoblasts $\rightarrow n$ Gymnospores"; or, for Haemosporidia or *Aggregata*, "$n$ Sporoblasts $\times\, mn$ Gymnospores (Sporozoites)."

In the Gregarines, with the acquisition of an intercellular trophic stage, it became possible for the gametocytes to associate and become encysted together, so that the gametes are formed in a confined space, and there is no possibility of the male gamete failing to find the female. In correlation with this condition the differentiation of the gametes becomes less important, and, as Léger has pointed out, conjugation takes place prematurely between immature gametes, a condition which, carried further, has probably led to the complete isogamy of such forms as *Monocystis.*

In Coccidia the trophozoites remain intracellular, and hence the gametocytes are usually kept apart, though occasionally premature association takes place (*Adelea*, etc.). Correlated with this state of things, a very great specialisation of the gametes is brought about. In the female gametocyte the process of multiplication to form gametes is in abeyance, and each female gametocyte becomes a female gamete after elimination of nuclear substance. The male gametes, however, are produced usually in large numbers from the gametocyte (only when there is precocious association of gametocytes is the number of male gametes reduced), and the gametes themselves are of a highly specialised type. Thus the probability of a male gamete finding a female is very great, even if not a certainty, as in the Gregarines. Immediately after fertilisation the zygote divides to form the sporoblasts, which may be compared to those of Gregarines by supposing that the process of multiplication by which the gametocyte of the Coccidia gave rise primitively to a number of female gametes has not been completely suppressed, but merely deferred until after the process of zygosis.

From this point of view the female gamete of the Coccidia must be compared not to a single female gamete of a Gregarine, but to the whole number of those produced from a female gametocyte in the latter, the actual process of cell-division being temporarily arrested. This interpretation receives the strongest support from some remarkable observations recently made by Schaudinn [51*a*] upon the life-cycle of the Coccidian, *Cyclospora caryolytica*, parasitic on the mole. In this form, as described above (p. 225), the nucleus of the macrogamete normally throws off two "reduction-nuclei" which degenerate, and the reduced pronucleus then copulates with *one* of the numerous microgametes which penetrate the female gamete (see p. 227). But in a large number of cases Schaudinn observed that the reduced pronucleus underwent degeneration, while the reduction-nuclei, on the contrary, flourished and continued to divide, populating the macrogamete with a large number of nuclei. In such cases, when the usual swarm of microgametes entered the macrogamete, each microgamete copulated with one of the numerous nuclei of the macrogamete, the result being a process of multiple fertilisation of the macrogamete, round which an oöcyst is secreted in the usual way. There can be no doubt that, as Schaudinn suggests, this multiple fertilisation is, from the phylogenetic point of view, a reminiscence of an ancestral condition in which the female gametocyte produced numerous female gametes, each capable of being fertilised by a microgamete. The effects of this multiple fertilisation upon the *Cyclospora* are, however, purely pathological, and lead to a complete degeneration of the contents of the oöcyst, which shrink and break up, with production of a great quantity of brown pigment, in a way that recalls the so-called "black spores" of the Haemosporidia (p. 253). This is a striking instance of a pathological condition resulting from a reversion to an ancestral mode of development.

It follows from the homologies put forward above between the gametes of Coccidia and those of Gregarines, that the cyst of the latter is a formation functionally analogous, but not phylogenetically homologous, to the oöcyst of the former. In both types, however, the contents of the cyst are to be regarded as equivalent, and the sporoblasts and spores (gymnospores or chlamydospores) as strictly homologous in the two cases. The first impulse towards the divergent evolution of the reproductive phases of Gregarinida and Coccidiomorpha respectively probably came from the acquisition, by the former, of an intercellular trophic phase. There is, however, another group, the sub-order *Haemosporea*, in which an intercellular trophic phase has been acquired, and in which similar adaptations in the reproductive phases might be expected to occur, but since next to nothing is known at present with regard to the sexual reproduction of these forms, it is impossible as yet to say how far such expectations are fulfilled.

## SUB-CLASS NEOSPORIDIA.

*Sporozoa in which reproduction goes on during the trophic phase.*

### ORDER 4. **Myxosporidia.**

The Myxosporidia are one of the most populous and abundant groups of the Sporozoa, exhibiting a wide range of structural variations, correlated with great divergence in habitat and mode of life. They are nevertheless a well-defined and homogeneous order, characterised more especially by the following points of organisation and development:—The trophozoite is amoeboid and Rhizopod-like; spore-formation commences at an early period and proceeds continuously during the growth of the trophozoite; the spores are produced *endogenously*, *i.e.* within the protoplasm of the trophozoite; and each spore always possesses one or more very distinctive structures, the "*polar capsules*," which have a strong resemblance to Coelenterate nematocysts. These points taken together are sufficient to distinguish one of the Myxosporidia (including under that term the Microsporidia or *Glugeidae*) from any other sporozoan type.

(*a*) *Occurrence, etc.*—The Myxosporidia, and especially their spores, figure in older zoological works under the names either of "fish-psorosperms" or of "pébrine-corpuscles." The former name, applied to the sub-order *Phaenocystes* (=*Myxosporidia sens. strict. auct.*), arose from the fact that the Ichthyopsida are the group of animals most favoured by their attentions; the latter name, denoting various species of *Cryptocystes* (=*Microsporidia*, Balbiani), was given on account of the well-known association of one species with the destructive silkworm-disease, "la pébrine."

The *Phaenocystes* are pre-eminently parasites of Vertebrata,[1] and especially of fishes. They are not known to occur in Amphioxus, in Cyclostomes, or in Ganoid fishes, and a few families of Teleostean fishes, such as the *Cyclopteridae* and *Pleuronectidae*, apparently do not harbour any Myxosporidia; but with these few exceptions the greater number of, at any rate, the commoner species of Elasmobranch and Teleostean fishes are subject to their attacks, and not infrequently one species of fish may be infested by four or five different species of Myxosporidia. They occur commonly also in various Amphibia, especially in Anura. In Reptiles they are less abundant, but *Myxidium danilewskyi*, Laveran, infests the kidneys of tortoises (*Emys lutaria* and *Cistudo europaea*), and an undetermined species has been described from the muscles of lizards and tortoises.[2] A "psorosperm" is also reported from the crocodile.[3] But up to the present, no Myxosporidia of any kind are known to occur in warm-blooded Vertebrata, in which the Sarcosporidia seem to take their place.

The Cryptocystes, on the other hand, are most commonly found infesting Invertebrate hosts, and especially Arthropods. Hence they were termed by Balbiani "psorospermies des Articulés." But they have also been found in other classes of animals both Invertebrate and Vertebrate. *Glugea laverani*, Caull. et Mesn., infests two species of Polychaetes; an undetermined species of *Pleistophora* has been found by Léger (1897) in a Trematode (*Brachycoelium* sp.); *Glugea helminthophthora* (Kef.) is found in tapeworms, *Taenia* spp., and in Nematodes (*Ascaris mystax*); *Glugea bryozoides* (Korot.), Thél., has been described by Korotneff from the Bryozoan *Alcyoncellum fungosum;* while a number of species of *Glugea* and *Pleistophora* are known from various fishes. The range of this sub-order is therefore wide, and future researches will probably show it to be even more extended than it is known to be at present.

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[1] Exceptions are:—*Chloromyxum diploxys*, Thélohan (*Cystodiscus diploxys*, Gurley), discovered by Balbiani in the moth *Tortrix viridanà*; an unidentified species of *Myxobolus* (?) discovered by Lieberkühn in the Oligochaete *Nais lacustris*, and figured by Bütschli, Bronn's "Thierreich," Pl. 38, Fig. 23; and the organisms described by Stolč as *Actinomyxidia* from aquatic Oligochaeta (*vide* p. 298 *infra*).

[2] Danilewsky, 1891, and Pfeffer, 1893; see Thélohan [113].

[3] Solger, 1877; see Gurley [102].

(*b*) *Habitat, Effects on their Hosts.*—The Myxosporidia, taken as a whole, seem to be more efficient than any other group of Sporozoa in impairing the health and vitality of their hosts, and are often the cause of the most virulent epidemics. The ravages of the pébrine disease amongst silkworms, caused by *Glugea bombycis*, is perhaps the most familiar example of their destructive powers, but many other instances could be cited, especially the frequent epidemics amongst fish caused by Myxosporidia both in Europe and America. The destruction wrought by *Myxobolus pfeifferi* amongst barbel, and by *M. cyprini* amongst carp, in the rivers of France and Germany, has caused a good deal of attention to be directed to the parasites in question, and in the case of the former, the investigations of Hofer and Doflein elicited some interesting facts. The barbel were found to be infested with the *Myxobolus* in all the rivers of Germany, but while in certain rivers, particularly in the Moselle, the parasite is endowed with powers so deadly that the barbel are killed off in thousands, elsewhere it is comparatively innocuous. The epidemics amongst crayfishes in France, caused by *Thélohania contejeani*, also deserve special mention. The economic importance of the Myxosporidia has led to their being the object of thorough and extended investigations in recent times. Ten years ago the Myxosporidia were an obscure group of which comparatively little was known; at the present day, though much remains still to be studied, they are perhaps more thoroughly worked out, and on the whole better understood, than any other section of the Sporozoa. To this result, the careful and laborious researches of Thélohan, Gurley, and Doflein have contributed more especially.

In the bodies of their hosts the Myxosporidia attack a variety of organs. The *Phaenocystes* are typically intercellular parasites, while the *Cryptocystes* commonly infect cells, but in the former sub-order the trophozoite in its earliest stages may occur either within or between cells (Doflein). The distinction has not, therefore, the importance often attributed to it. A large number of forms are tissue parasites, especially the numerous species of *Myxobolidae* amongst *Phaenocystes*, and many *Cryptocystes*. Hence the Myxosporidia, together with the Sarcosporidia, have been termed *Histosporidia* (Labbé) or *Histozoa*. These terms cannot, however, be used in any but a physiological sense, as a great many *Phaenocystes*, especially in the families *Myxidiidae* and *Chloromyxidae*, occur floating freely in the internal cavities of certain organs. It is therefore more convenient to distinguish at the outset between species living freely, on the one hand, and those infecting cells or tissues, on the other hand. The "free" species occur more particularly in the cavities of biliary or urinary organs in Vertebrate hosts; that is to say, in the gall-bladder, bile-ducts, urinary bladder, or kidney-tubules. No species are known, however, which, like the Gregarines, occur free in the alimentary canal or in the general body-cavity of their host during the trophic period of the life-history. In the organs which they affect they are found floating freely in the urine or bile, or attached by their pseudopodia to the lining epithelium, but they do not injure the cells themselves, except indirectly, as, for instance, when they may be so numerous in a kidney-tubule as to obstruct the lumen, with pathological consequences to the organ. The species which attack tissues and cells may occur in all parts of the body, infesting usually either connective or muscular tissue. The only classes of tissue exempt from their attacks, so far as is known, are bone and cartilage. They are not known to occur in the testis of any host, and though they frequently attack the connective tissue and stroma of the ovary, they rarely penetrate the ovarian follicles, which happens, however, in the case of the silkworm-moth, with the result of producing hereditary infection. Nervous tissue also is very seldom affected by these parasites, but *Glugea lophii*, Dofl., attacks the ganglion-cells of *Lophius piscatorius*. It is amongst the tissue-infecting Myxosporidia that the most injurious parasites occur. A given species may either restrict its attacks to one particular organ or tract, or it may ravage impartially almost all parts of the body, and as a rule the destructiveness of a parasite is directly proportional to the extent of its range within the body of the host. In some cases, for instance, in that of *Myxobolus pfeifferi* of the barbel disease, bacteria have been suspected of aiding the Myxosporidian parasite to produce its fatal results; but according to Doflein, bacteria do not occur in the tumours produced by the *Myxobolus* until they have reached the stage of suppuration.

The tissue-infecting forms fall naturally into two subordinate categories. In the first place, the attacks of the parasite may be *concentrated* at one spot, in which case a cyst is usually formed round it by the adjacent tissues (Fig. 81). Within the cyst, the body of the

Myxosporidian may exhibit a certain amount of differentiation at its outer surface to form a limiting membrane or envelope. In the second place, the parasite may be spread over a considerable area of the tissue infected, producing the condition aptly termed by Thélohan that of *diffuse infiltration* (Fig. 82). In this case, the protoplasmic body of the parasite and the cells of the tissue are inextricably commingled, and as the former is gradually used up to form spores, a condition is finally reached in which the tissue is found to be infiltrated with vast numbers of spores lying isolated from one another, or in groups between the cells. The concentrated condition of the parasite is usually distinctly visible to the naked eye, as little spots in the tissues; the diffuse condition requires microscopic investigation in order to discover the parasite. Some species occur indifferently in either state, others only in one or the other condition.

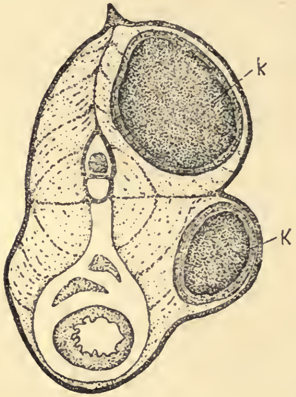

FIG. 81.
Transverse section of a stickleback (*Gasterosteus aculeatus*), showing two cysts of *Glugea anomala*, Moniez (*KK*), in the body musculature on the right side. (From Wasielewski, after Thélohan.)

Associated with the parasites in the tissues there are frequently to be found large numbers of "yellow bodies," the nature of which is doubtful; whether, that is to say, they are products of the parasite or of the host. They are often very conspicuous, and often enclose spores (see Doflein [100]).

An interesting fact was brought to light by Hofer and Doflein with respect to the destructive "Pockenkrankheit" of the carp. The disease shows itself in the form of large indurated tumours of the skin, consisting of epithelial growths which are invaded by leucocytes and by a proliferation of blood-vessels from the cutis. The most careful search failed, however, to discover parasites or intruding organisms of any kind in these tumours, but in all the diseased fish *Myxobolus cyprini* was found to occur plentifully in the spleen, liver, and kidneys. Hence these authors explain the skin-eruption of the carp as an indirect effect of the interference with the metabolism caused by the presence of the parasite in the internal organs, more particularly in the kidney. This view has, however, been sharply criticised, especially from the medical side (see Lühe [5], pp. 85, 86).

(*c*) *Morphology*. (1) *The Trophic Stage*.—The trophozoite of the Myxosporidia is remarkable, as has been said, for its amoeboid form and Rhizopod-like appearance. In all but very young forms, the body is divisible into two distinct regions, a denser external *ectoplasm*, clear and very finely granular, enclosing a more fluid *endoplasm*, which is opaque and coarsely granular (Figs. 83 and 84).

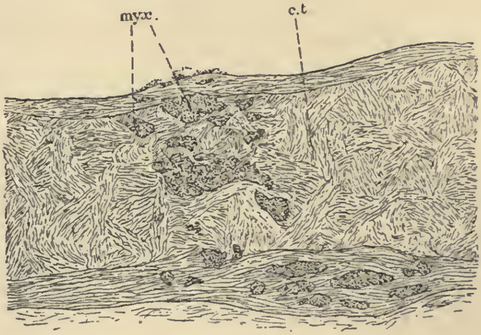

FIG. 82.

Section of the wall of the urinary bladder of a tench, showing *Myxobolus ellipsoides*, Thél. (*myx*), occurring in the condition of diffuse infiltration between the bundles of connective tissue (*c.t*). (From Wasielewski, after Thélohan.)

The ectoplasm is the seat of movement, and the pseudopodia take origin from it, but it also has a protective function, well seen in the forms inhabiting bile or urine, which disintegrate if the ectoplasm be damaged. The endoplasm, besides vacuoles, granules of various kinds, and sometimes crystals, contains the nuclei, and spores in all stages of development.

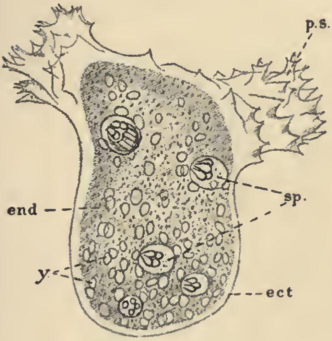

FIG. 83.

Trophozoite of *Chloromyxum leydigi*, Ming. (par. *Scyllium*, *Raia*, etc.), in a condition of activity. *ect*, ectoplasm; *ps*, pseudopodia; *end*, endoplasm; *y*, yellow globules in the endoplasm; *sp*, spores, each with four pole capsules. (After Thélohan, × 525.)

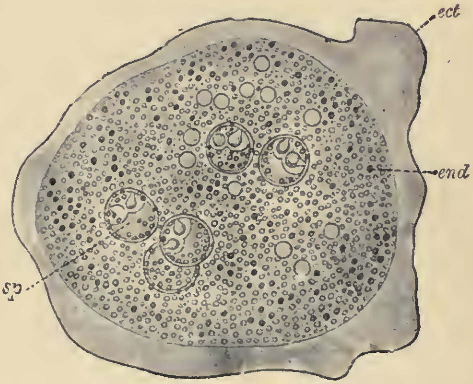

FIG. 84.

Trophozoite of *Sphaerospora divergens*, Thél. (par. *Blennius* and *Crenilabrus*). Letters as in Fig. 83. (After Thélohan, from Wasielewski, × 750.)

The pseudopodia are easy to observe in the free forms, but are less easily studied in the tissue-infecting species. They vary in form from lobose, rounded projections to slender or even filamentous processes, which may unite longitudinally, but never form reticular anastomoses (compare Figs. 84 and 86). They usually arise from the ectoplasm alone, but sometimes are formed as outgrowths of the whole body substance (Fig. 85). In many species, especially of Disporea, the pseudopodia are localised at the extremity which is anterior in locomotion (Fig. 87). In some of the forms which exhibit localisation of this kind, the anterior pseudopodia are not the principal agents in forward movement, but appear to be thrust out more or less tentatively, as it were, and progression is effected in the following remarkable manner. A strong tail-like pseudopodium grows out from the posterior end, which, as it is formed, pushes the body forwards (Fig. 87, *c*). The anterior pseudopodia at the same time bend round and elongate in proportion as the animal advances. The extension of the propulsive pseudopodium is accom-

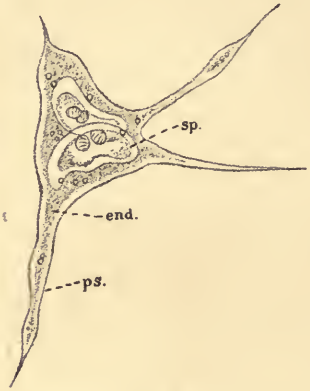

FIG. 85.

Spore-bearing trophozoite of *Ceratomyxa appendiculata*, Thél. (par. *Lophius* spp.). *ps*, pseudopodia ; *end*, endoplasm ; *sp*, spores. (After Thélohan.)

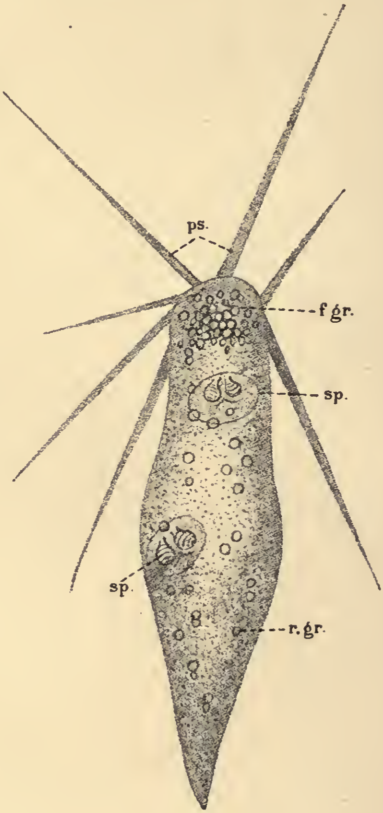

FIG. 86.

Spore-bearing trophozoite of *Leptotheca agilis*, Thél. (par. *Trygon* and *Scorpaena*). *ps*, pseudopodia localised at the anterior end ; *f.gr*, fatty granules similarly localised ; *r.gr*, refringent granules ; *sp*, spores, two in number. (After Thélohan, × 750.)

panied by the excretion of a granular substance which is left behind as the animal moves forwards. Locomotion effected in this manner, by means of a posteriorly situated propulsive pseudopodium ("Stemm-pseudopodium," Doflein) is unique amongst Protozoa, and possibly represents a primitive method of progression, which in the non-amoeboid Telosporidia is reduced to the shooting out of a secretion alone, without any extension of protoplasm, from the posterior end (see p. 181).

The pseudopodia, whatever their characters, are never used for the ingestion of solid food-particles, as in Amoebae. In free forms, however, they serve for fixation, as well as for movement. Besides amoeboid changes of form, the trophozoite may exhibit contractile movements like those of Gregarines, resulting in ring-like constrictions or flexions of the body.

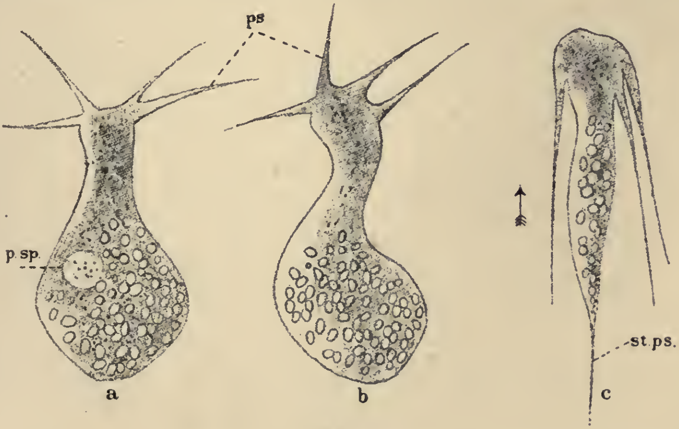

FIG. 87.

*Leptotheca agilis*, Thél., young trophozoites in which spore-formation has scarcely commenced, after Doflein. *a* and *b*, two figures of the same individual drawn at intervals of rather more than a minute. *c*, an individual moving forward (in the direction of the arrow) by means of a propulsive pseudopodium (*st.ps*) at the hinder end; the trail of granules left by the propulsive pseudopodium should be represented much longer. *ps*, pseudopodia; *st.ps*, propulsive pseudopodium; *p.sp*, pansporoblast.

In many cases, especially amongst encysted forms, the ectoplasm has its protective function developed at the expense of its motility, and becomes converted into a firm envelope, which may be finely fibrillar, as in *Glugea anomala*, or vertically striated, as in *Myxidium lieberkühnii* (Fig. 88). In the last-named species the character of the ectoplasm is variable, and in other cases it may give rise to lobose pseudopodia, or be covered with a sort of fur of fine non-motile filaments. These differentiations of the ectoplasm are important for comparison with the envelopes of the Sarcosporidia.

The endoplasm has a distinctly alveolar structure, and is sometimes vacuolated, and often coloured. It contains numerous enclosures and metaplastic products, most frequently of an oily or fatty nature, representing probably reserve nutriment. In the youngest trophozoites there is but a single nucleus, but with growth of the parasite the number of nuclei lodged in the endoplasm continually increases by their division, until many are present in the full-grown forms. The number is smallest in disporous forms (*infra*, p. 283), where it may be no more than ten, but usually it is much greater than this. The nuclei are very minute as a rule, generally not more than 1-2 μ in diameter, but they sometimes differ markedly in size in the same individual. Each nucleus consists in typical instances of a deeply-staining membrane enclosing a reticular framework, on which the chromatin is partly diffuse, partly aggregated towards the centre to form a "chromatosphere." True nucleoli or karyosomes are not found. The division of the nuclei takes place by a form of karyokinesis, but without asters or centrosomes (Fig. 89).

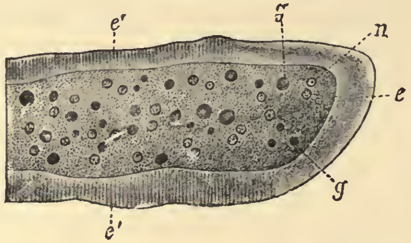

FIG. 88.

Extremity of a trophozoite of *Myxidium lieberkühnii*, Bütschli (par. *Esox* and *Lota*), in which no spores are as yet formed, × 750. *e*, *e'*, ectoplasm, homogeneous at *e*, vertically striated at *e'*; *n*, nuclei; *g*, globules of fat blackened by osmic acid. (After Thélohan, from Wasielewski.)

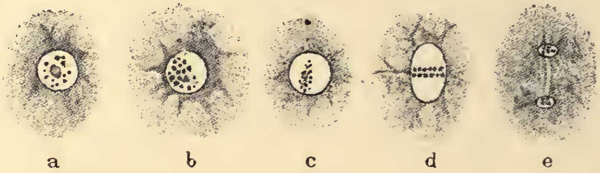

FIG. 89.

Stages in nuclear division in *Chloromyxum leydigi*, Ming. The resting nucleus (*a*) contains chromatin granules and a "chromatosphere." Preparation for division commences (*b*) by the breaking up of the chromatosphere. In the next stage (*c*) the chromatin collects towards the transverse plane of the nucleus, to form (*d*) the equatorial plate, which splits to furnish the chromatic substance of (*e*) the two daughter nuclei. (After Doflein.)

(2) *Spore-Formation.*—The spores commence to develop at an early stage in the growth of the trophozoite, and in some species they continue to be formed until the whole of the substance of the trophozoite is used up in their production. In other cases, however, the volume of the reproductive bodies is small in comparison with that of the whole body. The spores may be few in number,

no more than two being formed in some genera, hence termed *disporous*, but more usually they are produced in great numbers, and all stages of the development of the spores are commonly to be found present at the same time in a given individual. Since, therefore, sporulation does not, as in Telosporidia, indicate a cessation of growth and nutritive activity on the part of the parasite, it is not accompanied by encystment of the sporont. Occasionally, however, the ectoplasm may secrete a gelatinous envelope, when reproduction commences (*e.g. Myxidium giganteum*, Doflein).

In some cases, e.g. *Myxidium lieberkühnii*, Bütschli, spore-formation has been observed to vary with the seasons, being in abeyance in the winter, but proceeding actively in the warmer months.

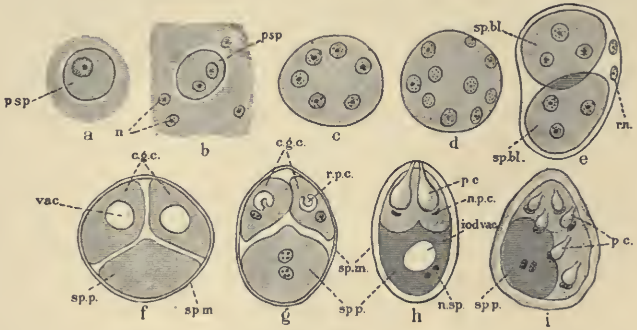

FIG. 90.

Stages in spore-formation. All the figures are from *Myxobolus ellipsoides*, Thél. (par. *Tinca*), except *a* and *f*, which are from *M. pfeifferi*, Thél. (par. *Barbus*). *a*, differentiation of the pansporoblast (*psp*). *b*, pansporoblast with two nuclei. *c* and *d*, pansporoblasts with six and ten nuclei respectively; in *d*, four of the nuclei are degenerating. *e*, pansporoblast segmented into two definitive sporoblasts, each with three nuclei. In the next four figures the definitive sporoblast, or the spore produced from it, is alone figured. *f*, definitive sporoblast segmented into three masses, the capsulogenous cells (*c.g.c*) and the sporoplasm (*sp.p*), within an envelope, the spore membrane (*sp.m*). *g*, more advanced stage. *h*, spore completely developed, with two polar capsules and sporoplasm containing an iodinophilous vacuole. *i*, abnormal spore containing six polar capsules. *psp*, pansporoblast; *n*, nuclei; *sp.bl*, definitive sporoblast; *r.n*, residuary nuclei; *c.g.c*, capsulogenous cells; *sp.p*, sporoplasm; *sp.m*, spore membrane; *vac*, vacuole; *r.p.c*, rudiment of *p.c*, polar capsule; *n.p.c*, nuclei of polar capsules; *iod.vac*, iodinophilous vacuole; *n.sp.*, nuclei of sporoplasm. (After Thélohan.)

The first sign of spore-formation is the concentration of protoplasm round one of the nuclei of the endoplasm, to form a little spherical corpuscle, the *pansporoblast* of Gurley ("primitive sphere" of Thélohan). Not all the nuclei of the endoplasm, however, are used up for the formation of pansporoblasts; a certain number may be left over as residuary nuclei, at least in the *Disporea* (Fig. 91). The pansporoblast is separated from the surrounding endoplasm by a thin pellicle or envelope of tougher protoplasm. In preparations a space may appear round it (Fig. 90, *a*), which is the result of shrinkage caused by preserving reagents, and is not present in the living condition. The nucleus of the pansporoblast divides repeatedly by mitosis, to form several nuclei, the normal number being about ten (Fig. 90, *b*, *c*, *d*). The protoplasm at the same time segments within the envelope into two masses, the definitive *sporoblasts;* this may take place before, or after, the full number of nuclei are formed in the pansporoblasts. The two sporoblasts when completely developed have each three nuclei, since four of the ten original nuclei are cast out as residuary nuclei, and undergo degeneration (Fig. 90, *e*). Each sporoblast now begins to secrete a cuticular *spore-membrane* at the surface, and within the membrane the protoplasm segments into three portions centred round each of the three contained nuclei (Fig. 90, *f*). Of the three corpuscles or cells thus formed, two are rather smaller than the third; the former are the two *capsulogenous cells;* the larger corpuscle is the *sporoplasm*, and its nucleus divides into two, a division which sometimes takes place at an earlier stage, so that the undivided sporoblast may contain four instead of three nuclei.

Each capsulogenous cell gives rise to a *polar capsule* in the following way. A clear spherical vacuole first appears near the nucleus of the cell. At some point, which is not constant, in the wall of the vacuole, a bud of protoplasm grows into the interior of the vacuole, pushing aside the clear substance contained in the latter (Fig. 90, *g*). The bud of protoplasm becomes a little pear-shaped body, surrounded by a clear envelope which is derived from the contents of the vacuole. At first connected by a stalk with the point at which it took origin, the pear-shaped body becomes free through severing of this connection, and then takes up a definite, specific orientation with regard to the spore as a whole (Fig. 90, *h*). At the surface of the pear-shaped body a membrane is formed, and in its interior a spirally-coiled filament is developed. The polar capsule, when fully formed, has a striking resemblance to a Coelenterate nematocyst, since the coiled thread can be shot out upon suitable stimulation (Fig. 97). Round the polar capsule are found the remains of the capsulogenous cell and its nucleus, but they soon degenerate and disappear.

When the development is completed, there are found, still contained in the envelope of the pansporoblast, two spores, each enclosed in a tough membrane, within which are the polar capsules and a little binucleate mass of sporoplasm which represents the single sporozoite. The envelope soon breaks down, and the spores are then found scattered in the endoplasm of the trophozoite.

The development above described is that typical for the *Phaenocystes*, but even in this order there is considerable variation, and in the *Cryptocystes* the deviations from the type above described are still more pronounced.

In the *Phaenocystes*, apart from individual abnormalities (Fig. 90, *i*), which are frequent, the chief developmental variations are seen in the number of polar capsules, of which there may be only one, or as many as four. The latter number characterises the *Chloromyxidae*, and in this family twelve or fourteen nuclei are found in the pansporoblast, and five or six in each definitive sporoblast (Doflein [100]).

In the *Cryptocystes* the pansporoblast always gives rise to more than two spores, namely, to four in *Gurleya*, eight in *Thelohania*, and to a large number in *Pleistophora* and *Glugea*. Further peculiarities are seen in the origin of the pansporoblast in this sub-order. In *Glugea*, numerous pansporoblasts are formed in each trophozoite, just as in the polysporous *Phaenocystes*, but in *Gurleya*, *Thelohania*, and *Pleistophora*, the whole trophozoite becomes converted into a single pansporoblast, thus producing a state of things which only differs from *Coccidium* or any other Telosporidian type in the fact that the spores are formed endogenously, in the bosom of the protoplasm, and not at its outer surface. An approach to this condition is also seen in the disporous *Phaenocystes*, where only one pansporoblast is formed in each trophozoite, the remaining protoplasm, with the contained nuclei, being left over as residual protoplasm which dies off ultimately (Fig. 91). It would not be safe, perhaps, to regard these forms which produce a single pansporoblast as connecting links in any way between the Telosporidia and the Neosporidia, but they are certainly suggestive in considering the relationship between these two sections of the Sporozoa. The Myxosporidia might be regarded as forms in which the trophozoite produces typically a greater or less number of sporonts (*i.e.* pansporoblasts) by a process of internal gemmation. On this view, the typical life-cycle of the Myxosporidia would represent an alternation of generations between trophic and reproductive individuals.[1]

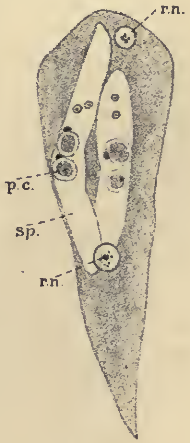

FIG. 91.

*Ceratomyxa inaequalis*, Dofl. (par. *Crenilabrus*), trophozoite containing two spores (*sp*) and two residuary nuclei (*r.n*). Other letters as before. (After Doflein.)

The development of the pansporoblast or sporont of *Thelohania mülleri* has been followed in detail by Stempell [111]. The nucleus divides without mitosis into eight nuclei, round which the protoplasm becomes segmented to form eight sporoblasts, imbedded in an intercellular residuum within the envelope of the sporont (Fig. 92, *a-i*). Each sporoblast becomes a spore, which has first one nucleus, later two (Fig. 92, *j-l*). Stempell has made the further remarkable discovery, that when a fresh host (*Gammarus*) is artificially infected, the spores remain some time in the gut before germinating, during which period the two nuclei divide, so that the spore ready to hatch has four nuclei (Fig. 92, *m*).

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[1] Since this paragraph was written (in 1901), Stempell [111, p. 265] has discussed the relation between "sporont" and "pansporoblast," and has suggested that the sporonts of *Thelohania* and similar forms are "pansporoblasts which in the course of the phylogenetic development have become independent individuals."

(3) *Morphology of the Spore.*—In their external form and structural details the spores of Myxosporidia show great variability, and furnish useful characters for purposes of systematic classification. The spore-membrane is composed of a transparent, homogeneous substance, of doubtful chemical nature, and remarkable for its resistance to the action of reagents. It has the form of two valves meeting in a suture, along which the spore opens to permit the escape of the sporozoite. The spore, as a whole, is very minute in the *Cryptocystes* (4 μ × 3 μ in *Glugea anomala*, 2·5 μ × 1·5 μ in *G. ovoidea*), and in this sub-order is uniformly pear-shaped. In the *Phaenocystes*, on the other hand, the spore is larger, and often of considerable size (100 μ × 12 μ in *Ceratomyxa sphaerulosa*), and it is always distinctly bilaterally symmetrical about the sutural or *vertical* plane. In *Leptotheca* and *Ceratomyxa* the spore is elongated in a direction at right angles to the plane of symmetry (Fig. 93); but in *Myxidium*, *Henneguya*, and most other genera of *Phaenocystes*, the longest axis of the spore lies in the plane of the suture (Figs. 95, 99, 107, etc.); a position intermediate between these extremes is occupied by the nearly spherical spores of *Sphaerospora* (Fig. 106). The spore-membrane may be prolonged into tails or processes of various kinds (Figs. 108, 112, etc.), which may attain a considerable length, in which case they are found coiled round while still

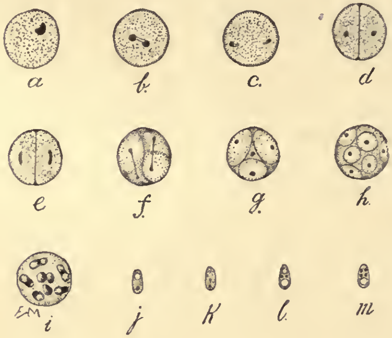

FIG. 92.

Spore-formation in *Thelohania mülleri* (L. Pffr.). *a*, sporont with single nucleus; *b*, *c*, division of the nucleus; *d*, first division of the sporont; *e*, the two nuclei commencing to divide again; *f*, further stage, the cells beginning to divide again; *g*, four-cell stage; *h*, sporont containing eight cells—sporoblasts—embedded in an intercellular residuum; *i*, the sporoblasts becoming spores; *j*, spore with single nucleus; *k*, nucleus of the spore dividing; *l*, spore with two nuclei; *m*, spore which has been three days in the gut of a new host, and which has four nuclei. After Stempell [111], × 2250.

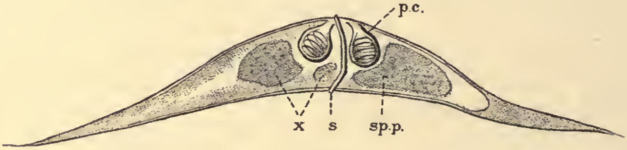

FIG. 93.

Spore of *Ceratomyxa sphaerulosa*, Thél. (par. *Mustelus* and *Galeus*), × 750, after Thélohan. *sp.p*, sporoplasm; *p.c*, polar capsules; *s*, suture; *x*, "irregular, pale masses, of undetermined origin."

within the pansporoblast envelope (Fig. 96), and become straightened out when set free from it.

The polar capsules are fixed to the valves of the spore-membrane close to the suture, and communicate each with the exterior by a fine canal, through which the coiled thread in the interior of the capsule can be shot out (Fig. 97). The natural stimulus which effects the discharge of the polar capsules is found in the digestive juices of the specific host infected by the parasite (see below, p. 290), but the same result can be brought about artificially by a number of reagents, such as ether, glycerine, boiling water, various acids, etc. When there is only one polar capsule, it marks a point commonly termed anterior. When there are two capsules, they may either be close together at the anterior pole, as in *Myxobolus*, etc. (Fig. 99),

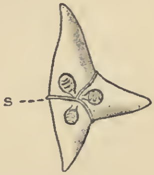

FIG. 94.

Abnormal spore of *Ceratomyxa truncata*, Thél. (par. *Clupea pilchardus*), with three polar capsules and three valves, after Thélohan. *s*, suture.

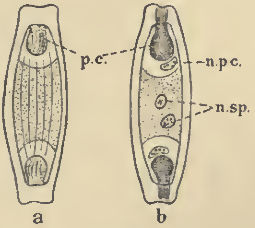

FIG. 95.

Spores of *Sphaeromyxa balbianii*, Thél. (par. *Motella* and *Cepola*), × 1500, after Thélohan. *a*, in the fresh condition ; *b*, fixed and stained, showing nuclei. *p.c*, polar capsules ; *n.p.c*, nuclei of polar capsules ; *n.sp*, nuclei of sporoplasm.

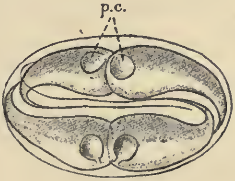

FIG. 96.

Two sister spores of *Ceratomyxa linospora*, Dofl. (par. *Labrus turdus*), still enclosed in envelope of the pansporoblast, showing the manner in which the long processes of the spore are curled round within the envelope. (After Doflein.)

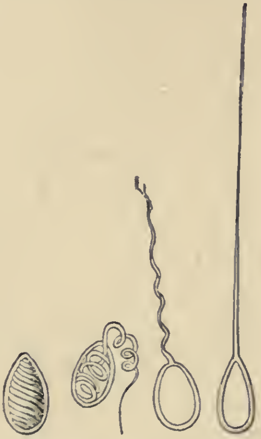

FIG. 97.

Polar capsules of *Myxobolus ellipsoides*, to show the ejection of the filament. (From Wasielewski, after Balbiani.)

or they may be situated at the two opposite poles, then termed inferior and superior, as in *Myxidium* (Fig. 107); perhaps a good example of a distinction without a difference. In *Chloromyxidae* four capsules are found, which again may be in one group at the anterior pole (Fig. 108), or disposed in two pairs at opposite extremities, after the fashion of *Myxidium*.

In *Glugeidae* the spores are remarkable for the fact that the single polar capsule is invisible in the fresh condition of the spore, hence the name *Cryptocystes*. It can, however, be demonstrated either by provoking the extrusion of the filament or by the action of certain reagents which render it distinct. The presence of a polar capsule in the spores of the *Glugeidae* was first made known by Thélohan, a discovery which threw light on the relationship of these forms, and led to the amalgamation in modern classifications of the *Myxosporidia* (*Phaenocystes*) and *Microsporidia* (*Cryptocystes*), formerly regarded as equivalent orders.

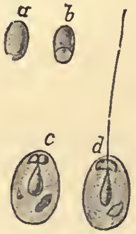

FIG. 98.

Spores of *Glugea bombycis*, Balbiani (par. *Bombyx mori*, etc.) *a*, *b*, spores seen in the fresh condition, × 1500. *c*, *d*, spores treated with nitric acid, which causes them to swell up and increase in size by a half, at the same time rendering the polar capsule distinct. In *d* the filament is extruded.

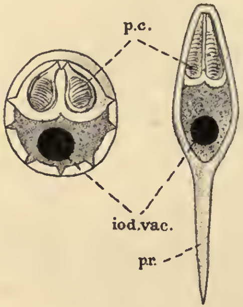

FIG. 99.

Spores of *Myxobolus mülleri*, Bütschli (on the left), and *Henneguya psorospermica*, Thél. (on the right), treated with iodine solution to show the manner in which this reagent colours the iodinophilous vacuole (*iod.vac*) characteristic of the *Myxobolidae*. *p.c*, polar capsules; *pr*, tail-like process. (After Thélohan, × 1500.)

The polar capsules are a very remarkable and distinctive feature of the spores of *Myxosporidia*, and have often been misunderstood. Mingazzini, for example, mistook them for the true sporozoites. It is nevertheless possible that the polar capsules may represent sporozoites modified and specialised for a particular function (for which see below, p. 290), as suggested by Delage. It is difficult either to criticise or to support this view until more is known of the relationship between the Myxosporidia and other types of Sporozoa.

The sporozoite, or *sporoplasm*, consists of a finely granular mass of protoplasm. There is never more than one such body, which has constantly two nuclei in *Phaenocystes*. In *Cryptocystes*, as we have seen, the nucleus, at first single, divides twice to produce four nuclei (p. 285 *supra*). The sporoplasm generally fills the spore completely, but in *Ceratomyxa* it is relatively small, and lodged in one valve of the shell (Fig. 93). In the family *Myxobolidae* the sporoplasm contains a peculiar vacuole, enclosing a substance which stains a reddish brown with iodine, and exhibits some of the reactions of glycogen (Fig. 99). No such vacuole is found in the other families of *Phaenocystes*, but in *Glugeidae* a clear vacuole is almost constantly present at the broader (posterior) extremity, which does not, however, exhibit any characteristic reactions. Besides this the sporoplasm of *Glugeidae* often contains numerous fine fatty globules.

(*d*) *Development of the Spores; Infective Processes.*—The developmental period which intervenes between the ripe spores and the youngest trophic stages, is the least known period of the life-cycle, as in all other Sporozoa, but the observations of Thélohan and Doflein make it possible to form a tolerably clear idea of the events that take place. The spores are set free from the parent trophozoite, apparently, by the death and disintegration of the latter in all cases, and we have next to consider the paths by which they leave the body of the host. In this process we may distinguish conveniently between natural and non-natural modes of exit. Thus in the case of species which live in the gall or urine of their hosts, the spores doubtless pass out of the body by natural channels. In the case of tissue-infecting forms, if the cysts are formed near the surface of the skin or the lining of the alimentary canal, they may excite suppuration, and so work their way to the adjacent surface when the abscess bursts, setting free the contained spores. In both these cases the death of the host is not necessary in order that the spores may be set at liberty; in the first case the host is not inconvenienced; in the second case a certain amount of damage is done, but not necessarily enough to destroy the host, which may live to harbour other parasites and to disseminate more spores. But in the case of species inhabiting more deeply situated tissues, the spores can only be set free by the death and disintegration of the host, and if this event be too long delayed, the result is fatal to the parasite; that is to say, the spores, if retained too long within the body of the host, pass their prime and die, as is so frequently the case in other Sporozoa which cannot leave the body of the host by natural means. The spores never, apparently, develop further in the host in which they are formed.

The spores when set free sink to the bottom of the water, when the host is an aquatic animal, or in other cases, as in that of the silkworm, are left lying about in the host's usual haunts. The infection of a new host is apparently always a casual one. The ingenious experiments of Thélohan [113] showed that the spores must be swallowed by the new host with its food, in an accidental manner, and pass into its alimentary canal; then, and not till then, under normal circumstances, does germination commence. Attempts to produce infection by direct inoculation, by means of intermediate hosts, or in other ways, were wholly unsuccessful. The first effect of the action of the digestive juices is the extrusion of the filaments of the polar capsules, which appear to act as organs of fixation, attaching the spore to the epithelium of the digestive tract. The two valves of the spore-membrane then separate along the suture and permit the escape of the contained sporozoite, which emerges as a minute amoebula and penetrates the wall of the digestive tract. From this point the tiny parasite embarks upon migrations, in some cases very extensive, in order to reach the organ or tissue which is its final destination. It is not possible to state with any certainty how these migrations are either effected or guided. In some cases the journey is perhaps performed on foot, as it were, the little amoeboid germ pushing its way actively through the tissues, like a leucocyte. In other cases the parasite may be passively transported by means of the blood-current. The latter method is probably the more usual, the little germ being carried along suspended in the blood-plasma; at any rate, there is no evidence that it ever attacks the blood-corpuscles. The one thing certain with regard to this stage of the life-history is that the parasite is able to select and to seek out, in some mysterious fashion, the specific organ or tissue which it affects, and which may be situated at a considerable distance from the original seat of infection.

Finally, it should be noted that in *Glugea bombycis* of the silk-worm disease, hereditary infection is effected by the penetration of the parasite into the ovary and the formation of spores within the ovum itself. Thus the newly-hatched silk-worms are already infected with the disease and disseminate it amongst healthy individuals. No other case of this kind is known in the Myxosporidia, nor indeed in the whole of the Sporozoa, with the possible exception of the parasites of Texas-fever (p. 262). In *Glugea bombycis* the infection of older caterpillars is effected exclusively by the accidental ingestion of spores along with the food, so that here too casual infection is the normal type, supplemented by hereditary transmission of the disease-germs.

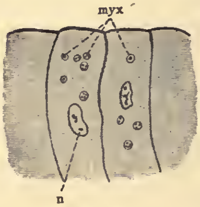

FIG. 100.

Kidney-cells of the carp infected with minute germs of *Myxobolus cyprini*, Dofl., which are multiplying rapidly. *myx*, the myxosporidian germs; *n*, nuclei of the kidney-cell. (After Doflein.)

(*e*) *Schizogony and Multiplicative Processes.*—When the amoebula reaches its definitive situation, it invades the tissues and commences to feed and to multiply endogenously with great activity. It is probable, however, that before the parasite arrives at its destination, it goes through developmental processes of which it is only possible as yet to form a conjecture. Doflein has drawn attention to the noteworthy fact that while the sporozoite of the *Phaenocystes* always contains two nuclei, the youngest observed trophic stages have but a single nucleus, and he has suggested that this difference is due possibly to conjugation, leading to an exchange and subsequent fusion of nuclei, taking place between the free amoebulae. No conjugation has been observed as yet in any stage of the life-history, and this fact makes it the more probable that some form of conjugation takes place at a very early stage, having in view further the great reproductive powers which these parasites exhibit even in the youngest stages of development. Conjugation at this early stage would find a parallel in the frequently occurring conjugation between swarm spores in many Rhizopods.[1]

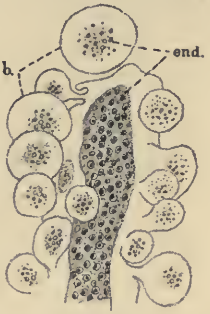

FIG. 101.

Formation of buds by multiple plasmotomy in *Myxidium lieberkühnii*, Bütschli (par. *Esox* and *Lota*), after Cohn. *b* buds; *end*, endoplasm; the clear outer portion represents the ectoplasm.

Like many other Sporozoa, the Myxosporidia possess the power of endogenous reproduction within the host, as well as of exogenous reproduction by means of spores. Doflein has aptly distinguished these two modes of reproduction as the *multiplicative* and the *propagative* methods respectively. The former is comparable in a general way to the schizogony of Telosporidia, though differing in details. It has long been suspected to occur in the Myxosporidia on account of the vast number of parasites that may be present in a given host, and the difficulty of supposing that each parasite could have originated in each case from a separate and independent spore infection. It is only in recent years, however, that it has been demonstrated by Cohn [99] and Doflein [100] in various forms. Multiplicative reproduction may take place in one of two ways. In the first place, it may go on in the full-grown trophozoite, either by simple binary fission, similar in externals to that of an ordinary amoeba, or by the formation of buds from the protoplasmic body.[2] Doflein has termed this process

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[1] According to Stempell [111, p. 262, footnote], Schaudinn has observed "copulation of the amoeboid germs of a spore" (*sic*) in *Glugea bombycis*. The publication of these observations will be awaited with interest. Stempell considers that the four nuclei seen by him in spores previous to germination (p. 285 *supra*, Fig. 92, *m*) represent a process of nuclear reduction preliminary to the conjugation.

[2] Laveran and Mesnil [106], however, deny that the budding described by Cohn occurs. They find that in *Myxidium lieberkühnii* endogenous multiplication goes on by equal or subequal plasmotomy in young trophozoites, and that these small forms often attach themselves to the surface of the body of large individuals,

*plasmotomy*, defined as the breaking-up of a multinucleate cell into multinucleate fragments; the plasmotomy may be either *simple*, *i.e.* ordinary fission, or *multiple*, as in budding (Fig. 101). This mode of reproduction is probably common in the free forms.

In the second place, multiplicative reproduction may take place in the youngest stages of the parasite, in the amoebula which has just reached its definitive situation. The nucleus of a minute individual undergoes a fragmentation into numerous daughter nuclei by a process of "multiple amitosis" (Fig. 102). The protoplasm then breaks up to form numerous minute uninucleate "swarm-spores," which spread the infection in the tissues of the organ affected, or it may be in all the tissues of the host, which in this way may be soon quite overrun by the parasite when once infected. This method of reproduction is probably very common, if not universal, in the tissue and cell-infecting *Myxobolidae* and *Glugeidae*.[1]

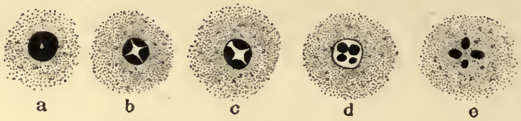

Fig. 102.

Stages of multiple amitosis in the youngest germs of *Glugea lophii*, Dofl. (After Doflein.) (The stages given here are those of a division into four, but the products of division may exceed, or fall below, this number.)

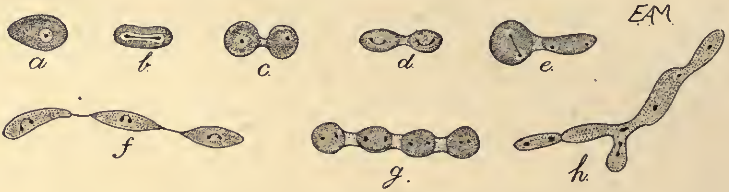

Fig. 103.

Schizogony of *Thélohania mülleri* (L. Pffr.). *a*, "meront" with single nucleus; *b* and *c*, division into two; *d* and *e*, into four; *f*, *g*, *h*, chains of meronts formed by rapid division. After Stempell, × 2250 (see footnote).

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thus giving rise to an appearance erroneously interpreted by Cohn as budding (compare Fig. 101). This method of reproduction goes on actively during the winter months, when no spores are produced.

[1] In *Thelohania mülleri* (L. Pffr.), from the muscles of *Gammarus pulex*, Stempell (*Zool. Anzeiger*, xxiv. p. 157) finds two kinds of trophozoites—larger *sporonts*, which produce spores, and smaller *meronts*, which multiply by a simple form of schizogony. Each meront divides into two after direct nuclear division, but before the separation of the two cells is complete, further division is commenced, so that three or four individuals are found connected in a group. This method of reproduction is clearly intermediate in character between the two methods, plasmotomy and formation of swarm-spores, described above.

[Since this note was written, Stempell's detailed memoir has appeared [111], from which Fig. 103 is reproduced.]

## CLASSIFICATION.

### Order **Myxosporidia**, Bütschli.

Sub-order I. Phaenocystes, Gurley (= *Myxosporidia sens. strict.*). Spores relatively large, bilaterally symmetrical, with two or four polar capsules, which are plainly visible in the fresh state. (Two anomalous species of *Myxobolus* have but a single polar capsule in the spore.) Two spores are formed in each pansporoblast. The trophozoite is an intercellular parasite in all but the earliest stages.

(*a*) *Disporea*, Doflein. Only two spores (*i.e.* one pansporoblast) are produced in each trophozoite. The greatest length of the spore is at right angles to the plane of symmetry, *i.e.* the sutural plane. Typically "free" parasites (see p. 277).

Family 1. Ceratomyxidae, Doflein. With characters as above.

Genus 1. *Ceratomyxa*, Thél., 1892. The valves of the spore-membrane have the form of hollow cones, the extremities of which are prolonged into more or less attenuated processes (Fig. 93). About nine species are known, all from the gall-bladders of fishes. Type-species *C. sphaerulosa*, Thél. (Fig. 93), from *Mustelus* and *Galeus*. Genus 2. *Leptotheca*, Thél., 1895. The valves of the spore membrane are not produced into long processes as in the preceding, and the sporoplasm fills the whole space within the spore-membrane not taken up by the polar capsules (Figs. 104, 105). Six species are known, four inhabiting the gall-bladders of fishes, while *L. ranae*, Thél., occurs in the kidneys of *Rana esculenta* and *R. temporaria*; *L. renicola*, Thél., in the kidney-tubules of the mackerel. Type-species *L. agilis*, Thél. (Fig. 104), from the gall-bladder of *Trygon vulgaris*.

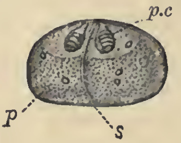

Fig. 104.

Spore of *Leptotheca agilis*, Thél. (par. *Trygon* and *Scorpaena*), seen in the fresh condition, × 1500. *p.c*, polar capsule; *s*, suture; *p*, sporoplasm. (From Wasielewski, after Thélohan.)

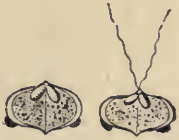

Fig. 105.

Spores of *Leptotheca perlata* [= *Chloromyxum* (*Sphaerospora*) *perlata*, Gurley] (par. *Acerina cernua*). (From Wasielewski, after Balbiani.)

(*b*) *Polysporea*, Doflein. More than two spores, usually a vast number, are produced in each trophozoite. The greatest length of the spore lies in the sutural plane.

While in general the Polysporea and Disporea are distinct enough in all their characters, a transition between these two sections is furnished by the genus *Sphaerospora*, which has nearly spherical spores, and of which one species, *S. elegans*, Thél., is disporous.

Family 2. Myxidiidae, Thél. The spores have two polar capsules, and are without an iodinophilous vacuole (p. 289) in the protoplasm. Typically "free" parasites.

Genus 3. *Sphaerospora*, Thél., 1892. (Characters, see above.) Four or five species are known, mostly from the kidneys of fishes, but

*S. masovica*, Cohn, is found in the gall-bladder of the bream (*Abramis brama*), and *S. elegans*, Thél., from *Gasterosteus* spp., penetrates from the kidney into the ovarian stroma. Genus 4. *Myxidium*, Bütschli. The spores are elongated in the sutural plane, and fusiform, with a polar capsule at each extremity (Fig. 107). The polar filaments are long and filiform. About seven species are known, the most familiar being *M. lieberkühnii*, Bütsch., from the urinary bladder of the pike. The other species are mostly from the kidneys or gall-bladders of fishes, but *M. danilewskyi*, Laveran, has been described from the kidneys of tortoises. Genus 5. *Sphaeromyxa*, Thél., 1892. The spores are fusiform and longitudinally striated, with truncated ends, and with a polar capsule at each extremity (Fig. 95). The polar filaments are short and conical. The trophozoite is generally of disc-like or lenticular form, with lobed ectoplasm at the margin. Three species are known from the gall-bladders of fishes. Genus 6. *Cystodiscus*, Lutz., 1889. Spores oval, with the sutural plane running obliquely to the principal axis, and a polar capsule placed near each extremity of the spore, but not quite terminal. Trophozoite similar to that of *Sphaeromyxa*. One species, *C. immersus*, Lutz., from the gall-bladder of *Bufo agua* and *Cystignathus ocellatus*, in Brazil. [By Gurley the species *Chloromyxum diploxys*, Thél., is also included in this genus, which is made the type of a family *Cystodiscidae*. The genus *Sphaeromyxa*, Thél., is also referred by him to this family, but doubtfully. By Thélohan, on the other hand, *Cystodiscus immersus* is referred to the genus *Sphaeromyxa*, and the genus *Cystodiscus* is not recognised.] Genus 7. *Myxosoma*, Thél., 1892. The spores are flattened, and oval in outline, with the polar capsules close together at the anterior extremity. One species, *M. dujardini*, Thél. (placed by Gurley in the genus *Chloromyxum*), from the gills of *Scardinius erythrophthalmus* and *Leuciscus rutilus*. Genus 8. *Myxoproteus*, Dofl., 1898. Spores roughly pyramidal, with spiky projections at the upper end (*i.e.* from the base of the pyramid), which bears two large polar capsules, separated by an interval equivalent

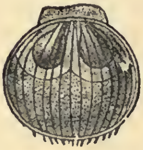

FIG. 106.

Spore of *Sphaerospora rostrata*, Thél. (par. *Mugil* sp.) (From Wasielewski, after Thélohan.)

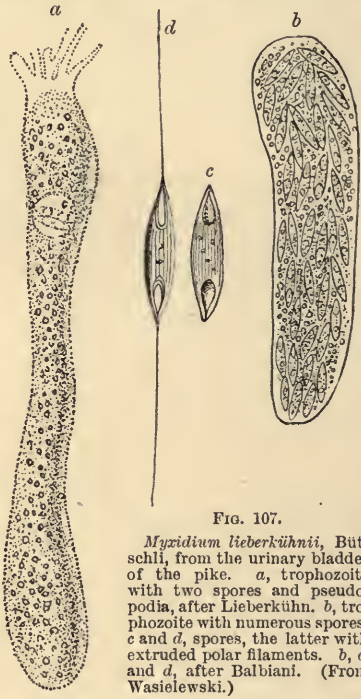

FIG. 107.

*Myxidium lieberkühnii*, Bütschli, from the urinary bladder of the pike. *a*, trophozoite with two spores and pseudopodia, after Lieberkühn. *b*, trophozoite with numerous spores. *c* and *d*, spores, the latter with extruded polar filaments. *b*, *c*, and *d*, after Balbiani. (From Wasielewski.)

to their own diameter. One species, *M. ambiguus* (= *Myxosoma ambiguum*, Thél.), from the urinary bladder of *Lophius piscatorius*.

FAMILY 3. CHLOROMYXIDAE, Thélohan. Spores with four polar capsules, and with no iodinophilous vacuole in the sporoplasm. (By Gurley the name of this family is used in a different sense, and contains the genera *Ceratomyxa* and *Chloromyxum*, a sub-genus of the latter being *Sphaerospora*, which includes *Myxosoma*.)

Genus 9. *Chloromyxum*, Mingazzini, 1898, with the characters of the family. Six or seven species are known; type *C. leydigi*, Ming., from the gall-bladders of various Elasmobranchs (Fig. 108, *a*). *C. caudatum*, Thél., occurs in the gall-bladder of *Triton cristatus* (Fig. 108, *b*). *C. diploxys*, Thél., infests *Tortrix viridana*; aberrant in the matter of habitat, this species differs also from other species of the genus in having the four polar capsules arranged in two pairs at the opposite extremities of the spore, like a *Myxidium* with doubled polar capsules. It should probably be regarded as a distinct generic type.

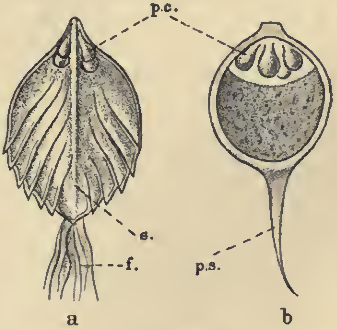

FIG. 108.

Spores of *Chloromyxidae*, after Thélohan. *a*, *Chloromyxum leydigi*, Ming., seen from the sutural aspect, × 2250. *b*, *C. caudatum*, Thél., × 1900. *p.c*, polar capsules; *s*, suture; *f*, filaments; *p.s*, tail-like process of the spore envelope.

FAMILY 4. MYXOBOLIDAE, Thélohan. Spores with one or two polar capsules, and with a peculiar iodinophilous vacuole in the sporoplasm. Typically tissue-parasites, only found in Vertebrates, with the doubtful exception mentioned above (p. 275, footnote).

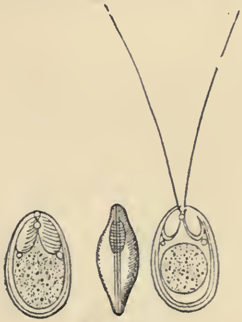

FIG. 109.

Spores of *Myxobolus ellipsoides*, Thél. The spores on the left and right are lying with the sutural plane horizontal, that in the middle with the sutural plane vertical. (From Wasielewski, after Balbiani.)

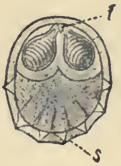

FIG. 110.

Spore of *Myxobolus mülleri*, Bütschli, in the fresh condition, ×1500. *s*, sutural margin, notched; *t*, triangular appendix of the valves. The filaments of the polar capsules are clearly seen. (From Wasielewski, after Thélohan.)

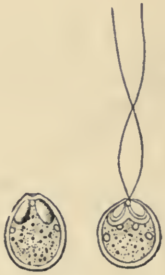

FIG. 111.

Spores of *Myxobolus* (?) *obesus*, Gurley (par. *Alburnus*). (From Wasielewski, after Balbiani.)

Genus 10. *Myxobolus*, Bütschli, 1882. Spore-membrane without a tail-like process, with one or two polar capsules (Figs. 109-111). About

40 species known, but not all named; found in the gills, fins, scales, kidney, spleen, etc., of various fishes, usually in the connective tissue of these parts. The genus is divisible into three sections; in the first come the aberrant forms *M. piriformis*, Thél., of the tench (*Tinca tinca*), and *M. unicapsulatus*, Gurley, from *Labeo niloticus*, which have pear-shaped spores, each with a single polar capsule; in the second are *M. dispar*, Thél., from *Cyprinus rutilus* and *Leuciscus rutilus*, and *M. inaequalis*, Gurley, from *Pimelodus blochi* and *P. clarias*, both with two polar capsules of unequal size; while in the third section are the very numerous forms characterised by two polar capsules of equal size, the best known being *M. mülleri*, Bütsch., the type-species (Fig. 99), from various fish (*Squalius cephalus*, *Barbus barbus*, *Phoxinus laevis*, *Crenilabrus melops*, *Thymallus vulgaris*); *M. ellipsoides*, Thél., of the tench (Fig. 109); *M. pfeifferi*, Thél., cause of the deadly barbel-disease; and *M. cyprini*, Dofl., from the carp. Genus 11. *Henneguya*, Thél., 1892. Spore with a tail-like process, with two polar capsules (Fig. 112). Four species are known, two of which infest sticklebacks (*Gasterosteus aculeatus* and *pungitius*); a third occurs commonly, with several varieties, in the pike and the perch. Genus 12. *Hoferellus*, Berg., 1898, nom. nov. for *Hoferia*, Dofl., 1898. Spore of broad and compressed form, with two tail-like processes at the posterior pole. One species, *H. cyprini*, Dofl., associated commonly with *Myxobolus cyprini* in the disease of the carp.

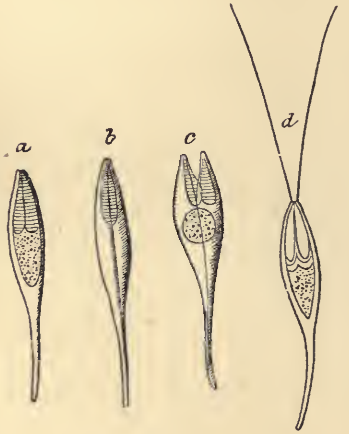

FIG. 112.

Spores of *Henneguya psorospermica*, Thél., from the pike. *a* and *d* are seen lying with the sutural plane horizontal; *b* and *c* with the sutural plane vertical. *c* is an abnormal spore.

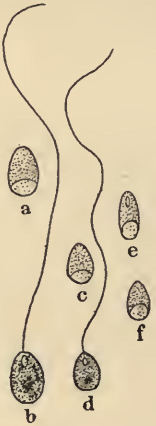

FIG. 113.

Spores of various *Glugeidae*, ×1500, after Thélohan. *a* and *b*, *Pleistophora typicalis*, Gurley; *a* in the fresh condition, *b* after treatment with iodine water, causing extrusion of the filament. *c* and *d*, *Thélohania octospora*, Henneguy; *a* fresh, *b* treated with ether. *e*, *Glugea depressa*, Thél., fresh. *f*, *G. acuta*, Thél.

SUB-ORDER II. CRYPTOCYSTES, Gurley (= *Microsporidia*, Balbiani).

Spores minute, pear-shaped, with one polar capsule, which is only visible after treatment with reagents (Fig. 113). More than two spores are formed in each pansporoblast. Cell parasites.

FAMILY 5. GLUGEIDAE, Thélohan. With the characters of the sub-order.

Section *α*. *Polysporogenea*, Doflein. The trophozoite produces numerous pansporoblasts, each of which in turn produces many spores.

Genus 13. *Glugea*, Thél., 1891. With characters of the section. (The synonymy of this genus is somewhat involved, and it is by no means certain that the name most commonly employed has the prior right over *Nosema*, Nägeli, 1857, or *Microsporidium*, Balbiani.) A large number of species are known, from a great variety of hosts, among which Arthropods and Fishes preponderate. The best known species is the destructive *G. bombycis* of the silkworm.

Section *β*. *Oligosporogenea*, Doflein. The trophozoite produces a single pansporoblast.

Genus 14. *Gurleya*, Doflein, 1898. The pansporoblast produces four spores. One species known, *G. tetraspora*, Dofl., from the hypodermic tissue of *Daphnia maxima* at Munich. Genus 15. *Thelohania*, Henn., 1892. The pansporoblast produces eight spores. Five species known, all from the muscles of Crustacea. Genus 16. *Pleistophora*, Gurley, 1893. The pansporoblast produces numerous spores. *P. typicalis*, Gurley, muscles of various fishes (Fig. 114); an undescribed species observed in a Trematode (Léger). Many of the numerous species described under the name *Glugea* are referred by Labbé to this genus.

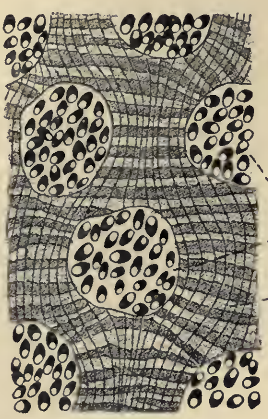

FIG. 114.

Portion of a section through a muscle fibre of *Cottus scorpius* invaded by *Pleistophora typicalis*, Gurley. *m.f*, muscle fibrils, retaining their striation; *myx*, cysts of the parasite, lying between the fibrils.

*Myxosporidia* (?) *incertae sedis.*—Under the name *Myxocystis ciliata*, Mrázek (1897 [110]) has described a parasite found in *Limnodrilus claparedianus*. The parasites in question were only observed in a single instance, occurring in vast numbers, and rendering the host opaque and greyish in appearance. They were found in the wall of the gut or in the body-cavity, as spherical or oval masses, 50 to 100 $\mu$ in diameter, often united in groups. They showed a distinct etoplasm, usually prolonged into a fur of delicate filaments, similar to those seen in many Myxosporidia (e.g. *Myxidium lieberkühnii*, p. 281). The endoplasm contained nuclei of different sizes, and also spores, the latter sometimes filling up the entire endoplasm. Each spore was oval, 4 $\mu$ in length, resembling a spore of *Glugea*, and contained a strongly refractile body, perhaps a polar capsule. Mrázek considers that *Myxocystis* shows some points of resemblance to the Sarcosporidia, and that its position is at present uncertain.

From certain freshwater Oligochaetes peculiar parasites have been described by Stolč [112], who regards these organisms as constituting a distinct group of animals, named by him Actinomyxidia, supposed to be intermediate in position between Myxosporidia and Mesozoa. Stolč's memoir is in Bohemian, but an abstract is given by Mrázek (*Zool. Centralbl.*, vii., 1900, p. 594), who considers these parasites to be Myxosporidia allied to *Ceratomyxa.* Stolč distinguishes three genera, *Hexactinomyxon*, *Triactinomyxon*, and *Synactinomyxon* (see Fig. 115 and description).

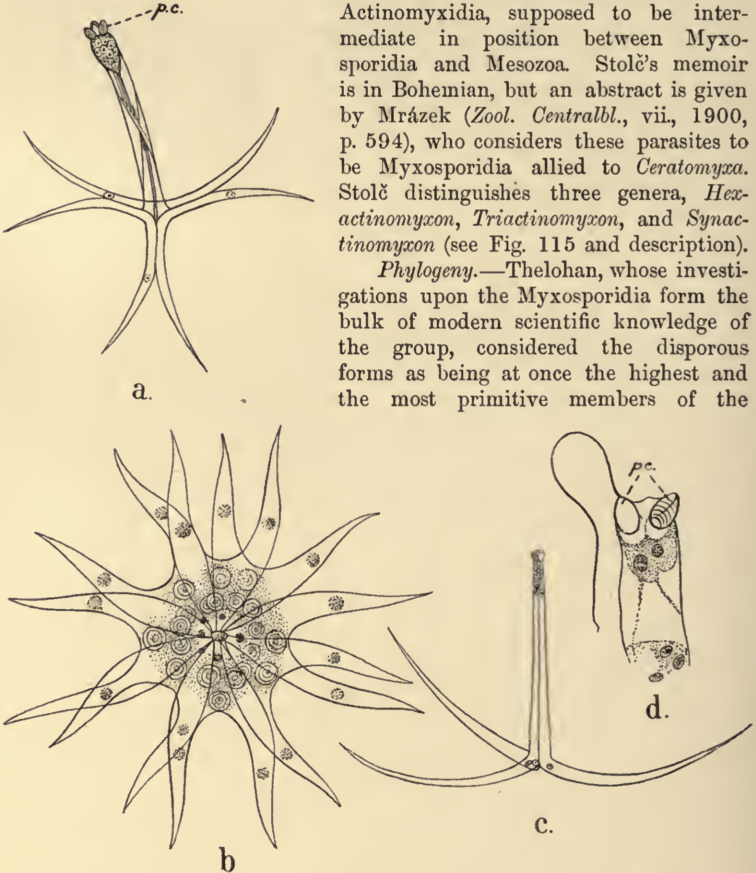

FIG. 115.

Figures of "Actinomyxidia," after Stolč [112]. *a*, *Hexactinomyxon psammoryctis*, Stolč (par. *Psammoryctes barbatus*). *b*, *Synactinomyxon tubificis*, Stolč (par. *Tubifex rivulorum*). *c*, *Triactinomyxon ignotum*, Stolč (par. *Clitellio* sp.). *d*, upper portion of *Hexactinomyxon* showing two of the three polar capsules, one with filament discharged.

*Phylogeny.*—Thelohan, whose investigations upon the Myxosporidia form the bulk of modern scientific knowledge of the group, considered the disporous forms as being at once the highest and the most primitive members of the entire order. The Disporea all live freely as amoeboid organisms in the bile or urine; they exhibit the greatest capacity for locomotion by means of their highly specialised pseudopodia, and their reproduction is perhaps of a primitive type in that each trophozoite produces but a single pansporoblast. The genus *Sphaerospora* connects them with the Polysporea, which on this view are to be considered as forms exhibiting adaptive degeneration due to their parasitic life. The tendency to such degeneration is to be regarded as having reached its culminating point in the tissue-infecting *Myxobolidae* and *Cryptocystes*, and, as in other parasites, it goes hand in hand with a great increase of the reproductive power, shown in the large number of spores produced by each individual.

It is hardly possible in the present state of knowledge to put forward any criticisms upon these interesting speculations until more is known of the relationship of the Myxosporidia to other Sporozoa. At the present they stand very much apart and isolated, and until intermediate forms are discovered linking them to other groups, it is not possible to decide which forms are to be considered as the most primitive in their organisation. As regards the reproductive capacity, however, it may be pointed out that on the whole it is distinctly related to the habitat of the parasite. Thus the Disporea all infest regions of the body in which their spores can pass to the exterior without difficulty by natural channels, and there is no danger of the spores becoming stale or dying off from too long retention within the body of the host, as so frequently happens in the tissue-infecting forms. In the latter, therefore, a much greater reproductive capacity is necessary to guard against the danger of staleness than in the former, in which no such risk exists. Not only is it necessary for the tissue-infecting forms to produce more spores, but also to keep up a constant supply of them, so that there may always be ripe spores ready to carry on the race when the opportunity for their dissemination arrives. These considerations do not, however, in any way invalidate Thélohan's conclusions.

## ORDER 5. **Sarcosporidia.**

The Sarcosporidia are the least known of all the chief orders of Sporozoa, in spite of the fact that, although restricted in occurrence, and also, apparently, as regards variety of genera and species, they are exceedingly abundant as individuals and very easily obtained as material for investigation. So far as it is possible in the present state of knowledge to characterise the group, their distinctive features are as follows. With the rarest exceptions, they are parasites of the striped muscles of warm-blooded vertebrates, birds and mammals. The trophozoite is an elongated body, which, in the earliest stages hitherto observed, is motionless, and is limited at first by a delicate cuticle, later by a thick envelope of complicated structure. Spore-formation commences at an early stage and proceeds during the growth of the trophozoite (hence Neosporidia), which may attain to a great size. The spores, which are produced in great numbers, are minute sickle-shaped or spindle-shaped bodies, with a very delicate envelope containing (1) the sporoplasm, with a single nucleus; (2) an oval striated body, placed at the pole of the spore, and representing, apparently, a polar capsule such as is found in the Myxosporidia. In some individuals, however, only naked gymnospores appear to be produced, probably serving for multiplication of the parasite within the host.

(*a*) *Occurrence, Habitat, etc.*—The Sarcosporidia have so far been found, with few exceptions,[1] only in warm-blooded vertebrates. In mammals they occur very frequently in domestic animals, and are nearly always to be found in the pig and the sheep. They also occur commonly in the horse and ox, and have been found in a number of other mammals, including the human species.[2] In birds they have been found in domesticated species, such as the common fowl and duck, and in wild birds, as, for example, the blackbird.

The earliest stage of the parasite which has been observed is lodged within the substance of a muscle-fibre in the form of an elongated body known as a "Miescher's Tube" (Fig. 117). The muscles affected are more especially those of the trunk in the vicinity of the stomach; the muscles of the oesophagus are the chief seat of the parasite (Fig. 116), then those of the larynx, the body-wall, and the diaphragm, and the psoas muscles. In acute cases all the skeletal muscles may be infected, even those of the head. Sometimes the parasites are found in the eye-muscles. Within the muscle-fibre the parasite grows until it distends the fibre to five or even ten times its normal breadth, absorbing the contractile substance as it does so. Finally, it is surrounded only by the sarcolemma and

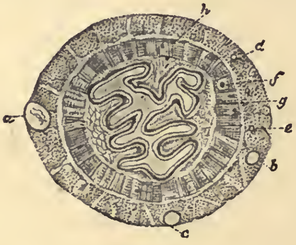

FIG. 116.

Sarcosporidia in the ox; a transverse section of the oesophagus, natural size, showing the parasites in the outer (*a*, *b*, *c*, *d*, *e*) and inner (*f*, *g*, *h*) muscular coats. (From Wasielewski, after Van Eecke.)

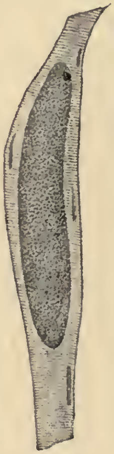

FIG. 117.

Longitudinal section of a muscle-fibre containing a Sarcosporidian parasite, ×60. (From Wasielewski, after Van Eecke.)

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[1] The exceptions are *Sarcocystis platydactyli*, described by Bertram from the muscles of the gecko, *Platydactylus mauritanicus*, and a species observed by Lühe in the lizard *Lacerta muralis*.

[2] For the recorded cases of Sarcosporidiosis in man, see Smith [121], p. 1, and Vuillemin [122], p. 1152.

sarcoplasm, the latter having greatly increased in amount, its nuclei multiplying by direct division (Laveran and Mesnil [119]). The parasite then passes from the substance of the muscle into the adjacent connective tissue, still surrounded, however, by a secondary coat derived from the muscle-fibre, in which the nuclei disappear. Thus the parasite is found under two phases, which have been given distinctive names under the impression that they represent distinct genera, the first lodged in the muscles (*Miescheria*), the second in the connective tissue (*Balbiania*).

In the second phase the parasite rounds itself off more, and the tissues of the host form an adventitious cyst round it. The cysts are conspicuous objects, often reaching a length of 16 mm. in the sheep, while in the roebuck (*Cervus capreolus*) cysts of 50 mm. in length have been observed. Within the cyst are formed vast numbers of minute germs (Fig. 120), either true spores or the so-called "Rainey's corpuscles" (see below). The cysts are observed to degenerate in some cases, their adventitious walls becoming calcified, as the result of a defensive process on the part of the host. Probably these are cysts containing spores, which can only develop in another host. In other cases, the cysts burst and spread their contents in the surrounding tissues, destroying the muscles and producing tumours and abcesses within which the parasite is found in the condition of "diffuse infiltration," like many Myxosporidian parasites. It is in this stage that the consequences may be dangerous or fatal to the host. The symptoms of Sarcosporidiosis in the pig are "paralysis of the hinder extremities, a skin-eruption, and general symptoms of sickness, such as thirst, increased body-temperature, and dim, streaming eyes."[1] The disease is sometimes the cause of fatal epidemics amongst domestic animals, especially sheep. In the mouse also *Sarcocystis muris* is a very deadly parasite. Mice attacked by it are distinguished by their puffy, bloated appearance (Koch [118]), and are soon killed by it.

Many observations tend to show that the dangerous effects of the Sarcosporidian parasites are not caused merely by the disturbances which they set up in the tissues of the host, but are due to an active poison secreted by the parasite itself. The indefatigable French naturalists, Laveran and Mesnil [120], have succeeded in isolating the toxin of the Sarcosporidian parasite of the sheep, and have named it *sarcocystin.* This substance is found to be extremely toxic to the experimental rabbit, since a demimilligramme of the fresh extract, containing $\frac{1}{10}$ milligramme of solid matter, kills one kilogramme of rabbit, with symptoms like cholera, in a very short time; in a feebler dose it produces a cachexy which usually ends fatally. In other animals the action of sarcocystin is more feeble and transitory in its effects.

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[1] Quoted from Wasielewski [7], from whom many other facts stated here are taken. The skin-eruption has an interesting parallel in the Myxosporidian disease of the barbel (see p. 278).

As regards the origin of Sarcosporidiosis, or the manner in which it spreads, nothing can be said definitely at present, but it is possible to put forward a few more or less probable surmises, which will be found below (p. 308).

(*b*) *Morphology and Evolution.*—The youngest examples of the trophozoite that have been observed had already attained a length of 40 $\mu$ with a breadth of 6 $\mu$ (Fig. 118, *a*). They are found as whitish opaque bodies limited by a fine, structureless cuticle. The protoplasm of the trophozoite is already in part segmented up to form a number of nucleated corpuscles or cells, which are evidently homologous with the primitive spheres or pansporoblasts of the Myxosporidia, and may therefore receive the same name.

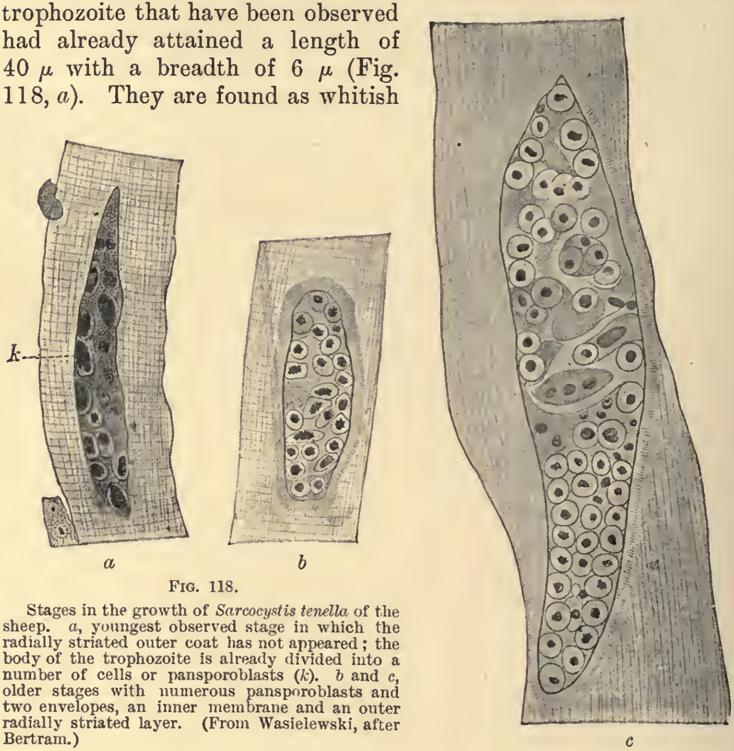

Fig. 118.

Stages in the growth of *Sarcocystis tenella* of the sheep. *a*, youngest observed stage in which the radially striated outer coat has not appeared; the body of the trophozoite is already divided into a number of cells or pansporoblasts (*k*). *b* and *c*, older stages with numerous pansporoblasts and two envelopes, an inner membrane and an outer radially striated layer. (From Wasielewski, after Bertram.)

In the next stage the parasite, still intramuscular in position, has increased in size and is surrounded by two coats (Fig. 118, *b*). The outer coat, which is thick and shows a fine radial striation, has received divers interpretations. While some observers regard the striation as due to the presence of fine pores or canalicules traversing a clear envelope, others, amongst whom are the most recent investigators, Laveran and Mesnil [119], declare the striation to be caused by a thick fur of fine filaments, planted vertically to the surface of the trophozoite, and serving to attach it to the fibrillae of the muscle-fibres. Both these views perhaps contain something of the truth; the external envelope probably arises from a stiff, radially striated ectoplasmic layer, such as is met with amongst some Myxosporidia,[1] which, by breaking down of the substance between the striations, is converted into a furry envelope. The inner coat is formed of a thin homogeneous membrane, prolonged externally into the filaments, and internally into the system of chambers previously described. Internally to the two coats lies the protoplasmic body of the trophozoite, comparable to the endoplasm of the Myxosporidia, and consisting

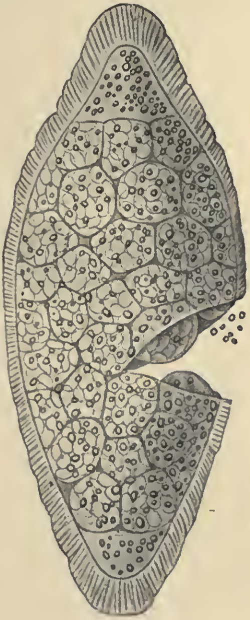

FIG. 119.

*Sarcocystis miescheriana* (Kühn) from the pig; late stage in which the body has become divided up into numerous chambers or alveoli, each containing a number of germs. (From Wasielewski, after Manz.)

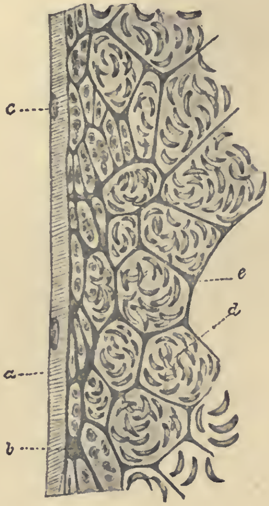

FIG. 120.

*Sarcocystis* of the ox; section of a stage similar to Fig. 119. *a*, substance of muscle-fibre; *b*, envelope of parasite; *c*, nuclei of the muscle; *d*, parasitic germs (gymnospores); *e*, walls of the alveoli. In the peripheral alveoli are seen immature germs. (From Wasielewski, after Van Eecke.)

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[1] Compare especially *Myxidium lieberkühnii* above, p. 281, Fig. 88.

almost entirely of numerous pansporoblasts (Fig. 118, *b* and *c*), which are continually being formed at the two poles of the trophozoite. Between the pansporoblasts, septa or partitions extend in from the inner coat, isolating them from one another, so that the entire endoplasm has a chambered or alveolar structure, each chamber containing originally a single pansporoblast (Fig. 119). Towards the centre of the body each pansporoblast has developed into a mass of spores or other germs, completely filling a chamber (Fig. 120); towards the poles pansporoblasts or early stages in spore-formation are found, and the two extremities of the body are occupied by the two regions of proliferation, so that the parasite grows by forming new spores at its two ends.[1]

In the third stage the parasite is encysted in the connective tissue, as above described. The body-form is less elongated, having become more or less rounded off, and the two polar areas of proliferation now extend round the whole trophozoite, forming a peripheral zone, the external layer of the body of the parasite, consisting of small alveoli, containing elements in process of development. Internally to the zone of proliferation are found alveoli crammed with ripe spores, which constitute an intermediate zone. The centre of the body is occupied by a granular substance, derived from disintegration of the centrally placed spores, which having become stale and past their prime, die and break up. The parasite continues to grow within the cyst, new spores being formed towards the periphery, to replace those which die off towards the centre. The development of the spores has not been followed in detail, but the pansporoblasts have at first one nucleus, later several.

The germs or reproductive bodies which arise from the pansporoblasts within the alveoli appear to be of at least two kinds, which may be conveniently distinguished as *chlamydospores* and *gymnospores* respectively.

The chlamydospores, commonly termed "spores" simply, are minute rod-like bodies, which vary in details of form and size in different species. In *Sarcocystis tenella* of the sheep (Fig. 122) they measure about 14 $\mu$ in length by 3 $\mu$ in breadth. One extremity is more rounded, the other pointed. The spore-membrane is very thin, and the chlamydospores themselves very delicate and fragile; they are easily acted upon by reagents, and even in distilled water they swell up and become globular. The pointed extremity of the chlamydospore is occupied by a clear space, about 5-6 $\mu$ in length, in which a delicate spiral striation can be seen in the fresh condition. The rounded end of the spore is almost filled by a large oval nucleus, containing a distinct nuclear corpuscle. The median portion of the spore is occupied by protoplasm with coarse granules. All the chlamydospores have the same structure.

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[1] Smith [121], in his recent account of the formation of gymnospores in *Sarcocystis muris*, gives a different interpretation of the various stages. He terms "sporoblasts" the "roundish or polyedral masses" which have been homologised above with pansporoblasts, and considers that the partitions between them are not ingrowths of the internal wall, but are "simply the walls of the sporocysts in close apposition with one another." He regards the gymnospores as sporozoites. Smith's terminology is the outcome of a misleading comparison of the Sarcosporidia with the Coccidia. He does not seem to have seen true spores.

The spirally striated body situated at the pointed end of the chlamydospore has great resemblance to a polar capsule of a Myxosporidian spore, but it is by no means certain how far the similarity extends. The most convincing proof of their similar nature would be the extrusion of the filament, which in Myxosporidia can be brought about artificially by a great number of reagents. It has been asserted by some investigators that a filament is extruded from the capsule of the Sarcosporidia also, and in support of this statement Van Eecke has published a figure,[1] which has had the effect of leading competent authorities to doubt the fact (see Laveran and Mesnil [119], p. 247; Lühe [5],

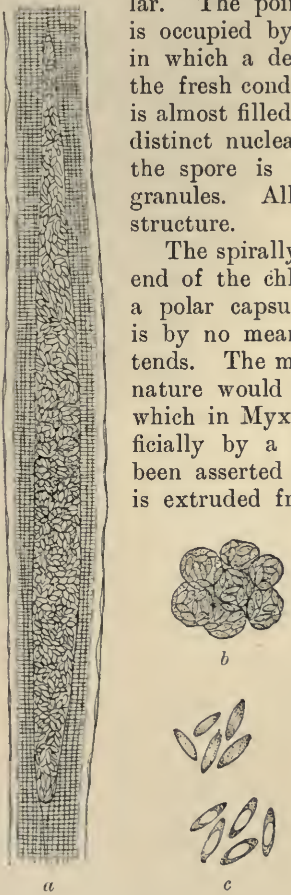

FIG. 121.

*Sarcocystis hueti* (Blanchard), from the muscles of *Otaria californica*. *a*, muscle-fibre containing a parasite, the body of which is chiefly made up of a vast number of gymnospores. *b*, clumps of gymnospores, each clump contained in an alveolus limited by a delicate membrane. *c*, different stages of the navicular gymnospores. (From Wasielewski, after Balbiani.)

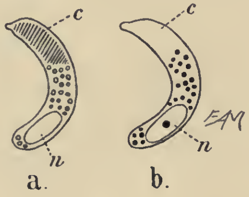

FIG. 122.

Spores of *Sarcocystis tenella*, Raill., from the sheep. *a*, spore in the fresh condition, showing a clear nucleus (*n*) and a striated body or capsule (*c*). *b*, spore stained by Heidenhain's Iron Haematoxylin method; the nucleus (*n*) shows a central karyosome; the striations of the polar capsule (*c*) are not visible. (After Laveran and Mesnil.)

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[1] Reproduced by Wasielewski [7] (Fig. 107, p. 125). Eight spores are shown, three of them with extruded filaments; of the latter, one has a single filament at the pointed end; the second *two* filaments at the pointed end; and the third *a filament at each end*. In the discussion following the reading of Koch's memoir [118], Wasielewsky has recently affirmed positively the extrusion of a polar filament from the spore.

p. 89). The allegation stands therefore in need of further support; the most recent investigators, Laveran and Mesnil [119], were unable to bring about extrusion of a filament from the spore. But although complete identity of structure has not been established, it is nevertheless extremely probable that the spirally striated body of the Sarcosporidian chlamydospore is strictly homologous (*i.e.* homogenetic) with the Myxosporidian polar capsule, and is an additional proof of the relationship between the two groups.

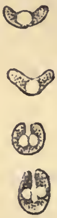
FIG. 123.
Gymnospores of *Sarcocystis miescheriana* of the pig, showing their changes of form. (From Wasielewski, after Manz.)

The gymnospores, commonly described under the names of "sporozoites" or "Rainey's corpuscles," vary a good deal in size and appearance (Figs. 120, 121, 123). Their form has been compared in different instances to that of a bean, kidney, crescent, sickle, or banana. In *Sarcocystis muris* they are about 12 $\mu$ by 4 $\mu$ in dimensions, but in other species they may be larger than this, or much smaller (3 or 4 $\mu \times 1$ $\mu$). Each consists of finely-granulated protoplasm, containing a nucleus, a few coarser granules, and sometimes one or two vacuoles. Those of *Sarcocystis muris* show active movements when warmed up to 35°-37° C. They perform gliding movements on a circumference corresponding to their own curvature, occasionally revolving also on their long axis, and thus producing "a boring or screw-like action" (Smith). In other cases they are said to become amoeboid under similar conditions. Both kinds of movement are probably to enable them to penetrate the tissues of the host.[1]

With regard to the significance of the two kinds of germs, and their destiny and further development, very little can be asserted definitely at present. The whole question of the reproductive bodies of the Sarcosporidia is, indeed, in a very confused state, and to generalise with regard to them is difficult, since no single observer seems to find more than one kind of spore. Those who, like Laveran and Mesnil, describe spores, say nothing about any gymnospores; and those who, like Smith and Koch, describe gymnospores, do not appear to be aware of the existence of any other kind of spore. It might be inferred from this that some species, such as *Sarcocystis tenella*, produce only chlamydospores, and others, such as *S. muris*, only gymnospores, but it is far more likely that both kinds are produced by the same parasite, sometimes the one, sometimes the other occurring, as the result of conditions as yet unknown. It is noteworthy in this connection, that *S. muris*, in which only gymnospores have been described, is of all species apparently the most deadly to its host, multiplying in it and overrunning the entire muscular system with fatal rapidity.

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[1] Besides the two kinds of germs described above, cysts have been described containing spermatozoön-like structures (see Wasielewski [7], p. 125), but from the accounts given it is difficult to form any clear idea of the nature of these bodies, or of their significance in the economy of the parasite.

It is certain that the parasites possess the power of multiplying to a dangerous extent in the tissues of their host, and it is still more certain that they are able to infect fresh hosts. From all that is known in other Sporozoa, it is reasonable to identify the naked gymnospores as the agents in the endogenous dissemination of the parasite, comparable functionally to the merozoites of *Coccidium*, and to regard the chlamydospores as destined for the infection of fresh hosts. Experimental proof of these hypotheses is as yet lacking, however. The only direct evidence bearing upon the dissemination of these parasites is that brought forward by Smith [121], who found that mice may contract the infection of *Sarcocystis muris* if fed with the flesh of a mouse infested with the parasite. It is extremely improbable, however, that this is the natural mode of infection. It would be difficult, as Smith points out, to account for the Sarcosporidia of cattle in this way. A parallel case of infection due to cannibalism has been described by Schaudinn for *Coccidium* (see p. 221). The chief point of importance established by the experiments of Smith is the fact that infection takes place by way of the digestive tract, as in the vast majority of Sporozoa. In this way the close proximity of the cysts, as a rule, to the oesophagus and stomach receives a simple explanation.

In Smith's experiments the gymnospores seem to have been the agents of infection, since he observed no other kind of germ, but it is probable that, in the natural method of cross-infection, it is the chlamydospores that are concerned. This conclusion receives further support from the facts stated above with regard to the death and disintegration of stale spores and their continual replacement by others freshly formed ; a state of things to which a parallel exists in the *Myxobolidae* and other tissue-infecting Myxosporidia (p. 289), and also in coelomic Gregarines. It may be reasonably inferred that in Sarcosporidia also the chlamydospores are not able to develop further in the host in which they are produced, but are in readiness for the moment when they can be transferred to another animal, failing which event, they become stale and perish. We have no clue, however, to the manner in which the cross-infection by the chlamydospores is effected, and nothing but surmises can be put forward.

The most remarkable feature of the chlamydospores is their extremely fragile nature. Unlike the very tough and hardy spores of other Sporozoa, those of Sarcosporidia betray a delicacy of constitution which must render them very unfitted to brave the elements outside the body of the host. For this reason many authorities[1] have expressed the belief that some intermediate host is required, as in the case of the malarial parasite, to convey the infection from one host to another. While this is an extremely probable hypothesis, no facts in support of it have been as yet discovered. But from the position of the parasite deep in the muscles of the host, it can hardly be a blood-sucking insect, as in the case of malaria, which spreads the infection. Three possibilities, at least, suggest themselves in this connection :—

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[1] Wasielewski [7], p. 126 ; Laveran and Mesnil [119], p. 248.

(1) That the intermediate host is a large carnivore of some kind, *e.g.* the dog, for the parasites of the pig or sheep.

(2) That, after death of the host, the parasites are taken up by some carrion-feeding animal, which might be either (*a*) a vertebrate, bird or mammal ; or (*b*) an invertebrate, such as the blow-fly or the burying beetle.

(3) That the infection might be taken on by some internal parasite of the vertebrate host, *e.g.* a flat-worm or nematode.

The third supposition is extremely unlikely. The second receives, perhaps, some support from the extremely toxic nature of the parasites themselves, which would be a property acting in their interests, by producing the death of the host. In any case there would still remain the question as to how the parasites reinfect the vertebrate host. It appears to be generally young animals that become infected, since the smallest trophozoite that has been described hitherto was found in a lamb eight months old, and it is extremely probable that the infection is by way of the digestive tract. Possibly, therefore, in the intermediate host the parasites form spores more resistent than those formed in the vertebrate host. A remarkable feature of the artificial infections effected by Smith was the long incubation period—40 to 50 days—which elapsed between the actual infection by feeding and the appearance of the parasite in the muscles. Evidently there is much still to be made out about these interesting parasites, and the field is one ripe for investigation.

(*c*) *Classification.* — Since Blanchard's genera *Miescheria* and *Balbiania* denote merely stages in the life-history of the parasites, they have become *nomina nuda*, and all Sarcosporidia are placed at present in a single genus :—

*Sarcocystis*, Ray Lankester, 1882, with the characters of the order. A great number of forms have been seen in different animals, many of which are probably distinct species, but only a few have received specific designations : such are *S. miescheriana* (Kühn), from the pig ; *S. tenella*, Raillet, from the sheep ; *S. platydactyli*, Bertram, from the gecko ; *S. muris*, Blanchard, from the mouse, etc.

(*d*) *Affinities.*—The nearest relationship of the Sarcosporidia is undoubtedly with the Myxosporidia, and with the sub-order Cryptocystes (Microsporidia, *Glugeidae*) in particular. The affinity is manifested in three points more especially—(1) the spore-formation proceeds continuously during the whole trophic stage ; (2) they are cell-parasites ; (3) the spores have a single polar capsule. The Sarcosporidia seem to be, in fact, the representatives of the Myxosporidia in warm-blooded hosts, and it is not improbable that in the future the two groups will be more closely united in systematic classifications.

## SPOROZOA INCERTAE SEDIS.

In addition to the five well-characterised orders of Sporozoa described in the foregoing pages, a certain number of forms have been discovered and described by various naturalists, which cannot be definitely inscribed in any of the above orders. To a large extent the uncertain position of these forms is due to the gaps existing in our knowledge of them. Just as certain genera, ranked in older treatises amongst those of doubtful affinities, have been referred, as the result of more extended studies, to a definite position in the classification of the Sporozoa—as, for instance, *Karyophagus* (p. 208) and *Piroplasma* (p. 269)—so it is probable that a more accurate knowledge of many forms now difficult to classify will bring to light unmistakable relationships between them and better known types. Other forms, again, will perhaps turn out not to be true Sporozoa at all. And finally, when these two classes of organisms have been sifted out, there will perhaps remain a certain number of types which must be ranked as orders truly distinct from any of those described above. Provisionally, three orders may be recognised, besides a certain number of very doubtful types.

### ORDER 6. **Haplosporidia**, Caullery and Mesnil.[1]

The forms comprised in this order agree in having a very simple developmental cycle, which in its principal features is as follows:—The youngest stage of the parasite is a minute rounded corpuscle with a single nucleus. With further growth the number of nuclei increase continually.[2] When full-grown the multinucleate body becomes divided up to form a mulberry-like mass, or "morula," of ovoid or spherical spores, each with a single nucleus, and with no trace of any sort of internal differentiation. From each spore arises one of the corpuscles, which was taken as the starting-point of the life-cycle. The following genera are referred to this order:—

Genus 1. *Bertramia*, C. and M., 1897, for *B. capitellae*, C. and M., from the body-cavity of *Capitella capitata*, and for the peculiar parasites occurring in the body-cavities of Rotifers,[3] first described by Bertram [116] in 1892; seen, *fide* Cohn [130], by Fritsch in 1895, and named by him *Glugea asperospora;* named by Zacharias, in 1898, *Ascosporidium*

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[1] The name of this order was written Aplosporidia by Caullery and Mesnil [128, 129], but was corrected to Haplosporidia by Lühe [5], since the word is evidently derived from ἁπλους, simple, and not from ἄπλους, unseaworthy.

[2] Caullery and Mesnil term the multinucleate trophozoite the plasmodium, but in the typical members of the order it has a definite body-form, and is not in any way amoeboid.

[3] These parasites were seen and studied by the present writer when working in Professor Bütschli's laboratory in Heidelberg in 1888. Extraneous circumstances prevented the completion of the studies upon them, and most unfortunately the drawings made of them were lost, but some permanent preparations were kept, from which the figures given above are drawn.

*blochmanni*; and recently studied by Cohn, *l.c.*, under the name *Bertramia asperospora* (Fritsch). The trophozoites in this genus commence growth as small rounded, uninucleate cells (Fig. 124, *g*, *h*), which become elongated, sausage-shaped, or cylindrical bodies in *B. asperospora* (Fig. 124, *a*-*c*), or flattened elliptical discs in *B. capitellae*, but in either case have a number of nuclei, which multiply as growth proceeds (Fig. 124, *i*, *j*). In *B. capitellae* the number of nuclei present in the full-grown parasite is from 40 to 80, but in *B. asperospora* it is less, from 25 to 35, as a rule; and the latter species is also characterised by the possession of large refringent granules in its protoplasm, which is limited by a distinct but delicate cuticle. When growth is completed, the body becomes segmented to form a mulberry-like mass of spores, each centred round one of the nuclei (Fig. 124, *d*, *e*).

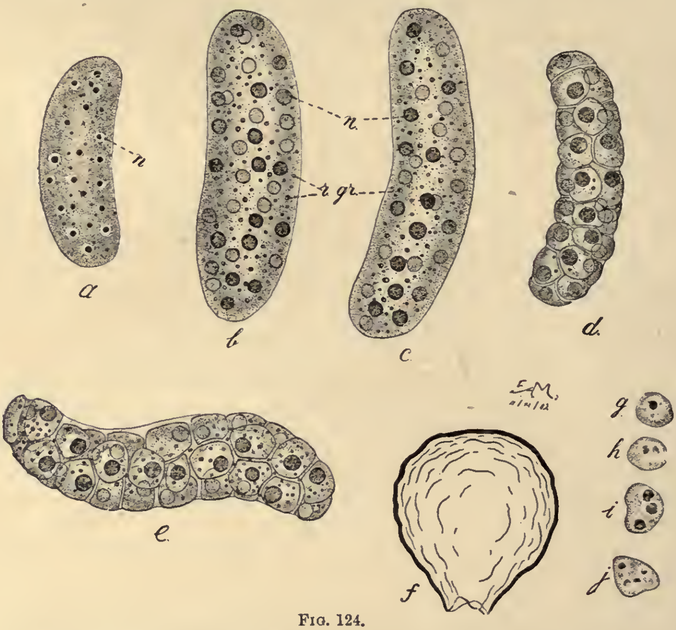

FIG. 124.

*Bertramia asperospora* (Fritsch), from the body-cavity of *Brachionus*. *a*, young form with opaque, evenly-granulated protoplasm and few refringent granules; the nuclei, which are difficult to make out clearly in the actual specimens, are small, and appear to be surrounded each by a clear space. *b* and *c*, full-grown specimens, with large nuclei and clearer protoplasm, containing numerous refringent granules (*r*, *gr*). *d* and *e*, morula stages, derived from *b* and *c* by division of the body into segments centred round the nuclei, each cell so formed being a spore. Between the spores a certain amount of intercellular substance or residual protoplasm is left, in which the refringent granules seem to be imbedded. The morula may break up forthwith and scatter the spores, or may first round itself off and form a spherical cyst with a tough, fairly thick wall. *f*, empty, slightly shrunken cyst, from which the spores have escaped *g*, free spore, or youngest unicellular trophozoite. *h*, *i*, *j*, commencing growth of the trophozoite, with multiplication of the nuclei, which results ultimately in forms such as *a* and *b*. Original figures, copied from drawings made with the camera lucida, × 1040. *a*-*c*, from one preparation, and from the same Rotifer. *d*-*j*, from another.

In *B. asperospora* the body-form of the morula is not different at first from that of the multinuclear trophozoite, except that its smooth contours are exchanged for a lobulated outline (Fig. 124). According to Bertram's observations, the sausage-shaped morula may now break up into its component cells or spores, which become scattered in the body-cavity of its host. The parasites observed by the present writer, however, were seen to round themselves off and assume a spherical form, a tough cyst-membrane then being formed round the whole mass (Fig, 124, *f*). Bertram also observed cysts in a single case. As the parasites are quickly fatal to their host, it is highly probable that rapid endogenous multiplication is effected by breaking up of the sausage-shaped morula and liberation of the spores without encystment, and that in other cases a protective cyst is formed. There appears to be no difference whatever, however, in the spores in either case, each spore being a small rounded uninucleate cell, limited by a delicate membrane. The spores are set free by the death and disintegration of the host, and are then swallowed by other Rotifers. In some way which has not been observed the spores pass from the gut into the body-cavity, and each becomes the starting-point of a fresh generation of the parasite. All stages of the parasite hitherto seen are perfectly motionless.

In *B. capitellae* the morula becomes encysted, and the contents of the cyst are divided up into compartments by trabeculae extending from the cyst-wall, formed apparently from residual protoplasm not used up to form spores. The alveolar condition of the cyst may be compared with that seen in Sarcosporidia.

Genus 2. *Haplo* [*Aplo-*]*sporidium*, Caullery et Mesnil, 1899, for *H. heterocirri*, C. and M., parasite of the body-cavity of *Heterocirrus viridis;* and *H. scolopli*, C. and M., parasite of the intestinal epithelium and perivisceral sinuses of *Scoloplos mülleri.* As in the last genus, a small uninucleate corpuscle becomes by growth and multiplication of nuclei the full-grown, multinucleate, but still unicellular trophozoite, measuring 100-150 $\mu$ in length by 20-30 $\mu$ in breadth. The body then becomes segmented into a "morula" of uninucleate cells. In *H. scolopli* each cell of the morula gives rise by further division to four uninucleate spores, but in *H. heterocirri* each segment of the morula becomes a single spore. In both cases the spores are distinguished from those of the preceding genus by the possession of a cap or operculum at one pole of the tough envelope, so that the spore resembles to a certain extent a poppy-capsule. In sea-water the operculum opens and sets free the contained sporoplasm.

Genus 3. *Coelosporidium*, Mesnil and Marchoux, 1897, for *C. chydoricola*, M. and M., from the body-cavity of *Chydorus sphaericus.* A uninucleate corpuscle grows into a multinucleate, sausage-shaped body, 60-100 $\mu$ in length by 15-20 $\mu$ in breadth, enveloped in a thick membrane, and containing centrally-placed fatty globules and refringent granules. Later the protoplasm becomes divided into segments corresponding with the nuclei, and forms eventually a cyst containing numerous spindle-shaped uninucleate spores. In addition, the spore-formation there appears to be an endogenous cycle, in which the protoplasm contains no refringent globules. The parasite castrates its host.

## ORDER 7. **Serosporidia**,[1] L. Pfeiffer.

This order was instituted by its founder for minute parasites observed by him in the body-cavity (haemocoele) of certain Crustacea. The following genera are referred here:—

Genus 1. *Serosporidium*, L. Pfeiffer, 1895. The type-genus of the order contains several species of oval or rounded parasites which reproduce in two ways—(1) By simple division; (2) by forming a cyst within which the parasite breaks up into numerous amoeboid germs. *S. cypridis*, L. Pffr., from the body-cavity of *Cypris* sp., and other species from *Cypris virens* and *Gammarus pulex*.

Genus 2. *Blanchardina*, Labbé, 1899 (nom. nov. pro *Blanchardia*, Wierzejski, 1890). Amoeboid masses, which become cylindrical or sac-like, and then of beaded form. Each bead becomes separated and forms a cyst, at first fusiform, later oval or spherical. Further reproduction not observed. Unique species *B. cypricola*, Wrzski., from body-cavity of *Candona candida* and *Notodromas monacha*.

Genus 3. *Botellus*, Moniez, 1887. Elongated ovoid tubes, containing halter-shaped spores, each with two nuclei. *B. typicus*, Moniez, from generative organs and haemocoele of *Ceriodaphnia reticulata*, *Chydorus sphaericus*, and *Moina rectirostris*. Two other species from *Cypris* and *Daphnia*.

Genus 4. *Lymphosporidium*, Calkins, 1900, for *L. truttae*, Calkins, parasite of the brook trout, *Salvelinus fontinalis*. The trophic phase of the parasite commences in the lymph as a minute germ which grows into an amoeboid body. The amoebula then invades the muscle-bundles of the intestine and other organs. In this situation the amoebula grows into the adult organism, which has its protoplasm full of chromatin granules, forming a distributed nucleus. Spore-formation commences by the parasite rounding itself off and being set free in the lymph or other cavities (gall-bladder, intestine), and by a concentration of the chromatin into several masses in the interior of the cell, each such mass becoming a spore. The spores are carried to all parts of the body in great numbers, blocking the lymph-passages, and causing sores and ulcers, and finally bringing about the death of the host. When set free the spores infect fresh hosts, probably by way of the digestive tract. In this situation they develop further, each producing eight germs or sporozoites, which become the starting-points of fresh generations of the parasites. The spores may, however, develop in the internal cavities of the host in which they were produced. This parasite causes extremely virulent epidemics.

## ORDER 8. **Exosporidia**, Perrier.

The order Exosporidia was founded by Perrier to include the peculiar organism, ectoparasitic upon certain aquatic Arthropoda, to which Cienkowsky gave the generic name of *Amoebidium*. Many authorities consider that the true systematic position of the forms is amongst the algae, and their place amongst the Sporozoa is far from being assured. Within the last decade, however, some other genera have been described which are possibly related both to *Amoebidium* and to the true Sporozoa, and the order may be retained provisionally for a collection of genera to which it is difficult to assign a more definite position. The genera placed here are best described separately.

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[1] The name was written Serumsporidia by Pfeiffer, and corrected to the more euphonious spelling, here adopted, by Wasielewski.

Genus 1. *Amoebidium*, Cienkowsky, 1861. The forms composing this genus differ in their habit of life from all typical Sporozoa and from any species mentioned in the preceding pages, being ectoparasitic upon various Crustacea or aquatic insect-larvae in freshwater. They were first discovered by Lieberkühn in 1856, who pointed out their affinities with "psorosperms." Five years later they were the objects of detailed investigation on the part of Cienkowsky, in whose opinion they were organisms of vegetable nature. Other species were added to the genus by later observers.[1] *A. parasiticum*, Cienk., the type-species (Fig. 125), occurs on the branchial lamellae, antennae, carapace, etc., of *Asellus aquaticus*, *Gammarus pulex*, and various freshwater Entomostraca, and upon *Phryganea* and other aquatic insect-larvae, in the form of slender tubes (Fig. 125, *a-e*). At one extremity the organism is attached to the skin of the host by a disc-like expansion, and immediately above this region the body is slightly narrowed to form a short stalk, continued by the rest of the tube, which is generally cylindrical and of even calibre, but may be clubbed or exhibit other variations as regards external form. The wall of the tube is a delicate membrane, which does not give the reactions characteristic of cellulose. The contents of the tube consist of protoplasm, containing fine granules, fatty spherules, and often vacuoles. The youngest tubes contain a single nucleus, but in older individuals the nuclei multiply as growth proceeds, and in full-grown tubes numerous nuclei are found scattered at regular intervals along the whole length of the tube (Fig. 125, *a*). The reproduction of *Amoebidium* is effected by two distinct methods, which may, however, be combined in various ways. In the first place, the contents of the multinucleate tube may be divided up by oblique partitions passing between the nuclei, into as many uninucleate segments or daughter-tubes as there were nuclei originally (Fig. 125, *c*). Each daughter-tube (Fig. 125, *b*) may then grow into a multinucleate *Amoebidium* again. In the second place, the whole contents of the multinucleate tubular body, or of the uninucleate daughter-tubes either before or after they have left the mother-tube, may become segmented along cleavage planes running in various directions, into a number of uninucleate amoeboid spores (Fig. 125, *d*, *e*), which soon begin to move about within the tube, and finally escape from it at one point or another. The amoebulae or "zoospores" (Fig. 125, *f-h*) thus liberated creep about for a time, but do not appear to feed, and have no contractile vacuole. After a time, each amoebula comes to rest, assuming first a spherical form, with one or two large vacuoles internally, then it becomes oval and forms a cyst (Fig. 125, *i-k*). In the warmer season of the year cysts are formed with a thin wall, within which the protoplasmic contents divide up in a few days to form a number of cylindrical germs, resembling sporozoites (Fig. 125, *k*, *l*). In the winter cysts are formed with a tough envelope, the contents of which remain dormant until the spring and then emerge. The contents of each such cyst, after liberation, may either become a young *Amoebidium* at once or may divide into two small *Amoebidia*, or may undergo the same development as the thin-walled summer-cysts (Fig. 125, *m*-*q*). Each of the sporozoites, as they may be termed, formed within the cyst becomes a young *Amoebidium* when liberated.

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[1] For references to the literature of the genus, see Bütschli [1], pp, 611-614, and Labbé [4], pp. 122, 123.

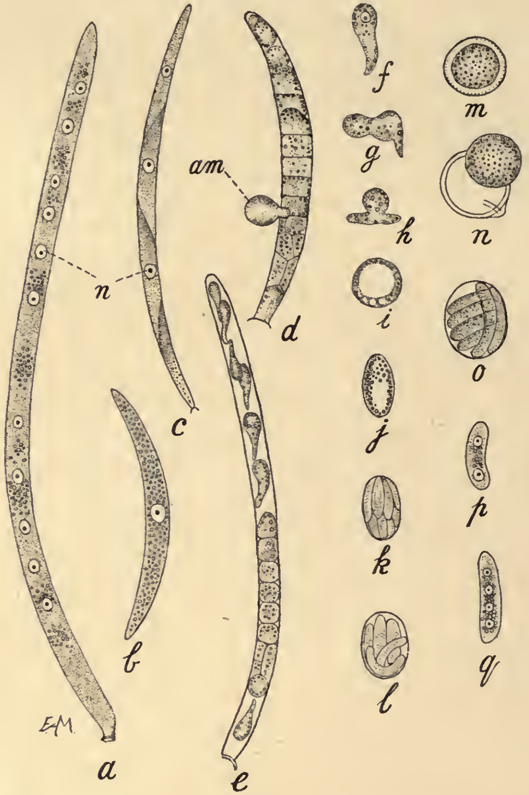

FIG. 125.

*Amoebidium parasiticum*, Cienk., phases of the developmental cycle. *a*, full-grown tube with numerous nuclei (*n*); *b*, young tube with a single nucleus; *c*, a tube divided up by oblique partitions into daughter-tubes; *d*, a tube divided up by transverse and longitudinal cleavages into amoebulae, one of which (*am*) is seen emerging from the tube; *e*, a tube containing freely moving amoebulae; *f*, *g*, *h*, free amoebulae; *i*, an amoebula come to rest and of spherical form, with a large vacuole; *j*, the form has become oval and the spore-membrane is beginning to appear at the surface; *k*, *l*, summer-spores, with sporozoites; *m*, a winter-spore, with thick cyst-wall; *n*, the contents of the winter-spore escaping; *o*, the contents of a winter-spore, which, after escaping from the cyst, have developed into a thin-walled spore containing sporozoites, similar to a summer-spore; *p*, *q*, young Amoebidia produced from sporozoites. (After Cienkowsky; *f*, *g*, and *h* are magnified 380 diameters, the other figures 285.)

Genus 2. *Siedleckia*, Caullery and Mesnil, 1898, for *S. nematoides*, C. and M., parasitic in the digestive tract of *Scoloplos mülleri* and *Aricia latreillei.* It occurs as a minute, worm-like creature (Fig. 126), attached by one extremity, termed proximal, to a cell of the intestinal epithelium. The body hangs free in the lumen of the gut, and performs various movements of torsion and flexion. Sometimes individuals are found unattached and progressing freely. The youngest stages are spindle-shaped and slightly curved, resembling sporozoites, with one or two nuclei (Fig. 126, *a*). As they grow in length the nuclei increase in number, keeping at first in single file (Fig. 126, *b-d*), but later forming several rows at the distal extremity of the body (Fig. 126, *e*). The full-sized parasite is about 150 $\mu$ in length and continues to elongate, but as it does so, small spherical segments, containing a variable number of nuclei, are constricted off from the distal extremity and detached (Fig. 126, *f*, *g*). Each of these becomes a young *Siedleckia*. No other method of reproduction has been observed.[1] The facts upon which to form a judgment with regard to the affinities of *Siedleckia* are therefore somewhat scanty. Labbé [130*c*] considers it allied to the Mesozoa, but it is difficult to see why. The general *habitus* of the animal is more like a Gregarine than anything else, and Caullery and Mesnil [8*b*] have noted its resemblance to the vermiform Gregarines, such as *Selenidium*, occurring in Annelids. The general description of *Siedleckia* and its reproduction reads (at least, to one who has not seen either of these forms) remarkably like the description of the

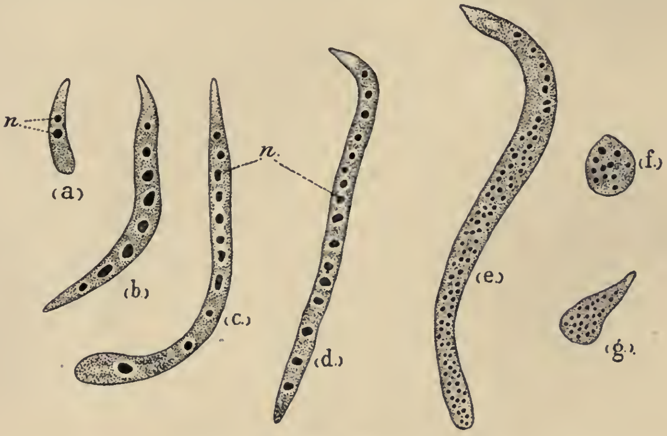

Fig. 126.

Phases of the life-cycle of *Siedleckia nematoides*, Caull. and Mesn. (par. *Scoloplos mülleri*, etc.). *a*, young stage, with two nuclei; *b*, *c*, *d*, older stages, with nuclei (*n*) still in single file; in *d* some of the nuclei are commencing to elongate in a transverse direction; *e*, full-grown individual, with very numerous nuclei; *f*, multinucleate spheres cut off from the distal extremity of a parasite such as shown at *e*; in *g* the sphere is commencing to grow into a vermiform *Siedleckia*. (After Caullery and Mesnil.)

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[1] It is by no means apparent how the multinucleate spheres detached as describe become the young forms with two or three nuclei, or whence the latter originate.

schizogony of *Schizocystis* given by Léger (see above, p. 191), and it is very possible that the true position of *Siedleckia* may be found eventually to be in or near the Schizogregarinae. To what extent it is at the same time allied to *Amoebidium* must remain an open question.

Genus 3. *Toxosporidium*, Caullery and Mesnil, 1900, for *T. sabellidarum*, C. and M., parasite of various *Sabellidae* (*Fabricia sabella*, *Oria armandi*, *Amphiglena mediterranea*, *Jasmineira elegans*, and *Myxicola dinardensis*). This form may conveniently be considered in connection with *Siedleckia*, although its affinities are extremely doubtful. Its discoverers approximate it provisionally to the coelomic Gregarines. It occurs in the form of motionless crescents lodged principally in the phagocytic cells of the body-cavity of the host. Each crescent has a nucleus containing two large crescent-shaped karyosomes. In the same hosts the intestinal epithelium contains "groups of spherules, which are perhaps the phase of endogenous multiplication of these parasites," the spherules being supposed to fall into the peri-intestinal blood-sinus and develop into the crescents. No other stages are known.

Genus 4. *Joyeuxella*, Brasil, 1902, for *J. toxoides*, Bras., parasite of the intestinal epithelium of *Lagis koreni.* The youngest stage of the parasite is a crescent-shaped intracellular body containing a nucleus with a large karyosome, and near the nucleus a small body resembling a micronucleus, and sometimes also another one further off. With further growth the nucleus multiplies, and the full-grown crescents have very numerous small nuclei. The body then divides up into numerous small elements. The further development has not been followed, but the epithelium of the same hosts also contains bodies resembling cysts of microgametes. Brasil considers that this form has some points of resemblance to *Gonospora*, *Selenidium*, and *Toxosporidium;* to *Siedleckia*, from which it differs in form, immobility, and intracellular habitat; but that on the whole it shows more affinities with Coccidia than with Gregarines.

Genus 5. *Exosporidium*, Sand, 1898, for *E. marinum*, Sand, an ectoparasite observed, in a single instance, on the leg of a marine Acarus at Roscoff. The parasite has a general resemblance to *Amoebidium*, being attached by one extremity of the cylindrical body, which becomes slightly narrower towards the free distal extremity. The dimensions given are 193 $\mu$ in length by 23 $\mu$ in breadth at the fixed extremity, 17 $\mu$ at the free end. The body is limited by a distinct membrane, within which the protoplasm is divisible into (1) an ectoplasmic layer resembling that of Gregarines, clear and free from coarse granulations; (2) a granular endoplasm containing six nuclei disposed in a longitudinal series. Two kinds of movements were observed—flexions, followed by sudden straightenings, of the whole body, and slow torsions of the free extremity. Sand considers this organism to be a Sporozoön, allied to *Amoebidium.*

The following genera are of quite uncertain position amongst the Sporozoa, if indeed they are Sporozoa at all:—

*Metchnikovella*, Caullery and Mesnil, 1897, for certain minute parasites infesting the endoplasm of certain Gregarines. The first phase of the parasite is a number of small nucleated corpuscles lodged in a vacuole of the endoplasm; the corpuscles multiply by fission, forming Streptococcus-like bands, which spread through the host; finally, fusiform cysts are formed, arranged with their long axis parallel to that of the Gregarine, and containing a number of nucleated corpuscles. The fusiform bodies probably represent the resistent phase which serves to infect fresh hosts. The type is *M. spionis*, C. and M., from *Gregarina* (*Polyrhabdina*, Ming. = *Selenidium*, Giard ?) *spionis*, Kölliker, parasite of *Spio martinensis.* Other species are known from the Gregarines of other Annelids.

*Hyalosaccus*, Keppène, 1899, for *H. ceratii*, Kepp., a parasite of various Dinoflagellata. As it is described by its discoverer in the Russian language, the reader anxious for further information is referred to the original memoir [130*b*].

*Rhaphidospora*, Léger, 1900, for *R. le danteci*, Lég., parasite of the intestinal cells of *Olocrates gibbus.* Specimens of this beetle, which belongs to the family *Tenebrionidae*, are found, in which the epithelial cells of the mesenteron are filled with rods resembling the rhaphides of plants, lodged in vacuoles and arranged parallel to the axis of the cell. Each rod is about 14 $\mu$ in length by 1·5 $\mu$ in breadth, and consists of a fine membrane enclosing deeply-staining filiform elements, which apparently are four in number, each with a chromatin granule. The filiform elements become liberated and appear to multiply by transverse fission, but ultimately they grow into rods, each at first consisting of finely granular protoplasm and a nucleus containing a few chromatin granules. Each such body then surrounds itself with a membrane, and its contents break up into filiform elements. All stages of the parasite are capable of active movements. The rods are probably the agents by which new hosts are infected, through being swallowed with the food.

*Chytridiopsis*, Aimé Schneider, 1884, for *C. socius*, A. S., intracellular parasite of the intestinal epithelium of *Blaps mortisaga ;* sometimes occurring also within the Gregarine, *Stylorhynchus longicollis*, found in the same host. The youngest stage of the parasite is a small spherical protoplasmic body, which, according to Schneider, is without a nucleus, but it seems more probable, even from Schneider's figures, that it has numerous small nuclei. The parasite grows to a certain size and then becomes encysted. Within the tough, doubly-contoured cyst-envelope a zone of cortical granular protoplasm is separated off, and within this cortical zone, which appears to represent residual protoplasm, the body of the parasite divides up into a great number of simple spherical spores, about 1·5 $\mu$ in diameter and quite undifferentiated, forming a solid mulberry-like mass occupying the centre of the cyst. By its spores and general appearance *Chytridiopsis* seems to approach very nearly to the Haplosporidia.

*Chitonicium*, Plate, 1898, for *C. simplex*, Plate, parasite of the mantle-cavity and the epithelium of the mantle groove, foot, and gills of *Ischnochiton minator*, and infecting also less abundantly *Chaetopleura peruviana* and other chitons of Chili. It occurs as little oval or spherical cells, each with a distinct nucleus and cell-membrane, which multiply actively by direct amitotic division in the epithelial cells, causing great destruction amongst them. The parasites are also found free in the mantle-cavity, and multiply in this situation, where Plate thinks it possible that they may infect the eggs and embryos of the host, in which the mantle-cavity acts as a brood-pouch. No other stages of the parasite have been observed, since the spindle-shaped variety first described by Plate has been found by him, on renewed investigation, to be in reality a pathologically modified form of the nuclei of the supporting cells of the mucous frills. Since no method of sporulation has been shown to occur, this parasite cannot as yet be enrolled amongst the Sporozoa.

*Karyamoëba*, Giglio-Tos, 1900, for *K. renis*, G.-T., an intranuclear parasite (?) of the renal epithelium of *Mus decumanus.*

*Nematopsis*, A. Schneider, 1892, for *N.* sp., parasite of the connective-tissue cells of the mantle of *Solen vagina.* A single host-cell may contain one, two, or three cysts, in each of which is lodged a little coiled-up animalcule, resembling a tiny Nematode, but consisting apparently of a single cell with one nucleus.

Schewiakoff, in 1893 [135], described, but without naming them, certain "entoparasitic tubes" (Schläuche) occurring in *Cyclopidae* (*Cyclops* and *Diaptomus* spp.), where they had been discovered by Schmeil. These parasites occur as amoebae, free in all parts of the body-cavity (haemocoele) of the host. The amoebae (Fig. 127, *a*, *b*) vary in size from about 7 $\mu$ in length by 3 $\mu$ in breadth, to 20 $\mu$ by 6 $\mu$; they send out lobose pseudopodia, and possess each a vesicular nucleus and *a contractile vacuole*, a point in which they differ from all known Sporozoa. The contractions of the vacuole take place at intervals of about 30 seconds. The amoebae creep over the epithelial cells and the muscles; and they were observed to fuse with one another to form plasmodia (Fig. 127, *h*, *i*, *j*), varying in size according to the number of individuals thus united. Since sometimes plasmodia formed of two or three amoebae were observed later to contain only a single nucleus, it is highly probable that nuclear fusion also takes place in them. After a certain time encystment takes place, either of single amoebae or of plasmodia. In the former case the cysts are spherical (Fig. 127, *c*, *d*), containing one nucleus, and the contractile vacuole, which is visible for some time, its pulsations becoming slower. The cyst-membrane has a double contour. The nucleus now becomes divided up (Fig. 127, *e*), and the protoplasm becomes centred round the daughter-nuclei to form oval spores (Fig. 127, *f*, *g*). The plasmodia become encysted in a similar manner, but the cysts formed by them are larger and oval in form, and the breaking up of the nucleus and other preparations for spore-formation may take place while the plasmodia are still free (Fig. 127, *j*, *k*, *l*). The spores are formed progressively in the cysts; a cyst formed from a single amoeba was observed to contain, in about ten hours after the division of the nuclei was complete, six spores imbedded in protoplasm containing numerous free nuclei; twenty-four hours later the number of spores was doubled, with undifferentiated protoplasm and free nuclei still present in the cyst; and after another twenty-four hours the cyst was entirely filled by spores, with no residual protoplasm or nuclei. The spore-formation in plasmodial cysts took place in a similar manner. Each spore arises as a condensation of the protoplasm round a free nucleus, and when fully formed is an oval or pear-shaped body, 3·3 to 4 $\mu$ in length, strongly refringent and perfectly hyaline in appearance, limited externally by a thin pellicle, and containing a single nucleus at the broader end. The remarkable fact was observed that the spores multiply by fission in the cyst, their nuclei dividing by a process of karyokinesis which Schewiakoff has studied and figured in all its details, and which is followed by an oblique division of the whole spore (Fig. 127, *m-q*). Besides spores dividing in this way,

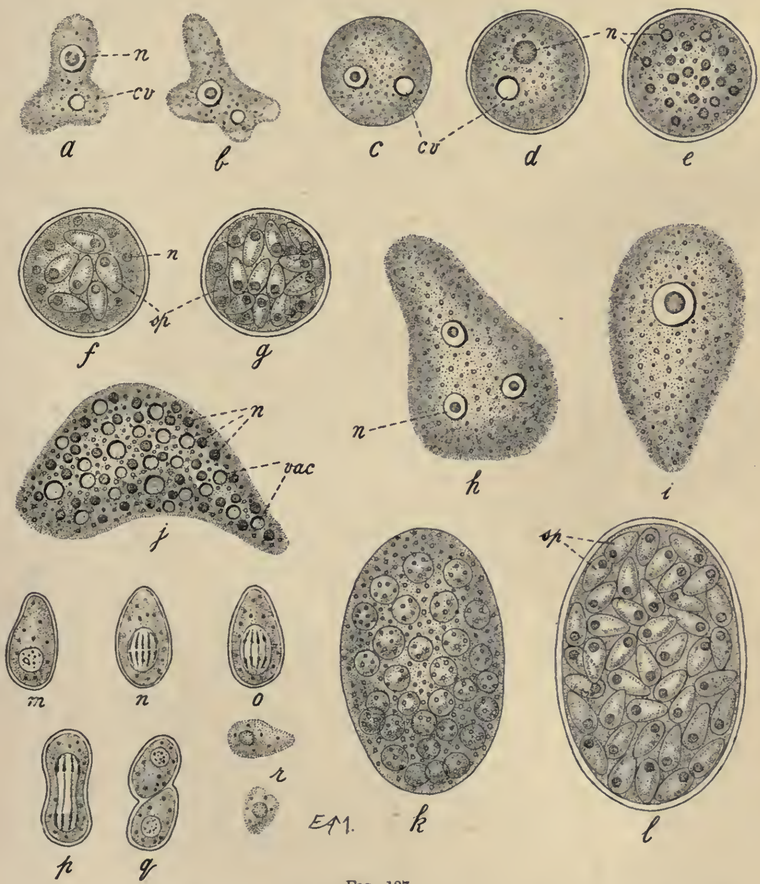

FIG. 127.

Phases of Schewiakoff's internal parasites of *Cyclopidae*. *a* and *b*, free amoebae; *c*, commencement of encystation; *d*, cyst with one nucleus; *e*, cyst with many nuclei; *f*, cyst one day old, with six spores (*sp*) and a number of free nuclei (*n*); *g*, cyst three days old, full of spores in a residual matrix; *h*, plasmodium with three nuclei; *i*, the same later, with one nucleus; *j*, plasmodium preparing for sporulation, with numerous nuclei and vacuoles (*vac*); *k*, encysted plasmodium, containing numerous spherical sporoblasts; *l*, later stage of the preceding, the sporoblasts having become ripe spores; *m-q*, stages in the division of a spore; *r*, small amoebulae liberated from spores. (After Schewiakoff [135], *a-l* × 1500; *m-r* × 2600.)

Schewiakoff found others attached in couples by their anterior extremities, and then frequently showing peculiarities in their nuclei which led him to suspect that conjugation may also take place between spores, but he was unable to confirm the existence of any such process. The spores are set free by bursting of the cysts and are to be found sticking to the muscles, but their further development was not followed, and it is not known how the *Cyclops* becomes infected with them.

As regards the systematic position of these interesting parasites, Schewiakoff thinks that "they should, without doubt, be placed amongst the Sporozoa." If so, however, they differ from all known Sporozoa, first in the possession of a contractile vacuole in the trophic stage, secondly in their tendency to form plasmodia, and thirdly in the power of multiplication by fission possessed by the spores. They have indeed a certain superficial resemblance to the species of *Thélohania* which are also parasitic on the muscles of Crustacea, but they differ from all Myxosporidia in the simple, undifferentiated character of the spores, a feature in which they resemble the Haplosporidia. If the Sporozoan affinities of these parasites are, as they seem to be, undeniable, then they must be regarded as quite the most primitive members of the group, linking the Sporozoa in an unmistakable manner to the true Rhizopoda.

The systematic enumeration of the Sporozoa would not be complete without mention of the very numerous forms of supposed parasites described from various human diseases. A list of these doubtful organisms, with full bibliographical references, will be found in Labbé ([4] pp. 128-132), under the title "Pseudo-coccidies," and a bibliography, complete up to 1899, is given by Hagenmüller [3]. In the great majority of cases, if not in all, it is very doubtful if these bodies are parasitic organisms at all, so that to refer them definitely to the Sporozoa, and even to the Coccidia, as is commonly done, is in the highest degree premature. It is especially round the alleged parasites of cancer that the dispute has been hottest. The natural eagerness to fathom the causes of the most terrible of human diseases has produced a flood of literature in which the "discovery" of a parasite, and in many cases of a Sporozoan parasite, has been affirmed with complete confidence many times over. But although Korotnef in 1893 gave a complete description of the cancer-parasite in all phases of its life-history, under the name *Rhopalocephalus carcinomatosus*, the opinion has been steadily growing, and is now held by almost all zoological experts who have looked into the matter, that the bodies which revealed themselves to Korotnef and others as cancer-parasites are nothing more than cell-enclosures of various kinds, either degenerations of structures normal to the cell, such as nuclei, "Nebenkerne," etc., or products of abnormal cell-metabolism, supplemented perhaps by leucocytes and other cells in various states of diseased activity and degeneration. Recent expressions of zoological opinion have therefore been sceptical towards the parasitic theory of cancer, relegating the parasites to the realm of fable, or at least pronouncing decisively against their alleged Protozoan nature (see Doflein [2*a*], pp. 8-11; Schaudinn [51*a*], pp. 405-408).

Recently, however, the parasitic theory has been revived by Feinberg,[1] who asserts that in sections of young growing cancerous tumours, before the cells have begun to degenerate, there are to be found, *between* the proliferating tissue-cells, structures consisting of a membrane enveloping a protoplasmic body containing a nuclear corpuscle. Feinberg considers that these bodies are intrusive organisms totally distinct from the tissue-cells and their enclosures and products, and from his comparative studies upon the structure of the nuclei in various animal and vegetable tissues or unicellular organisms, he is further of the opinion that these parasites are indubitable Protozoa. The parasitic theory of cancer is therefore by no means dead yet; but the Sporozoan nature of the alleged parasites is far from being proved.

## THE AFFINITIES AND PHYLOGENY OF THE SPOROZOA.

In recent times no zoologist has called in question the position universally assigned to the Sporozoa amongst the Protozoa. The attempts that have been made to establish kinship for them outside this sub-kingdom can scarcely be said to belong to modern zoology. The question remains, however, to which of the other classes of Protozoa the Sporozoa are most nearly allied. Assuming, as every evolutionist must, that all parasites are descended from free-living, non-parasitic ancestors, the problem that presents itself is to determine as far as possible the nature and affinities of the ancestral Sporozoa and their relationship to the three remaining classes of Protozoa—the Rhizopoda, Mastigophora, and Infusoria respectively. It may be said at once, however, that the Infusoria (Ciliata and Suctoria) need not be considered in this connection, since the Sporozoa exhibit no characteristics linking them specially to this very well-defined group.

Two rival theories of Sporozoan ancestry have been put forward by competent authorities—the one claiming for them descent from the Rhizopoda, the other from the Mastigophora. In considering these opposing views, it should be borne in mind at the outset that the Rhizopoda and Mastigophora are two classes which are connected by many links, and may be said almost to merge into one another at certain points. Many Rhizopoda have swarm-spores, or other stages in their life-cycle, which are flagellated; many Mastigophora, on the other hand, are amoeboid. Such forms as *Mastigamoeba* can only be distinguished from true Rhizopoda by the retention of a flagellum in the free stages of the life-cycle; were the flagellum lost, when adult, as in other cases, the organism would be classed as a Rhizopod. The distinction between the two classes is, therefore, somewhat arbitrary and artificial when the lowest members of them are taken into consideration. But the forms further from the boundary-line, in each class, are distinct enough, and if a typical member of either group be selected, such as *Amoeba* for Rhizopoda, and *Euglena*, or some similar form, for Mastigophora, we are confronted by two sharply contrasted types. It would indeed simplify the comprehension of the two theories of Sporozoan ancestry if they were termed the hypotheses of the *amoeboid* and the *euglenoid* ancestry respectively.

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[1] "Zur Lehre des Gewebes und der Ursache der Krebsgeschwülste," *Deutsche med. Wochenschrift*, xxviii. (1902), No. 11; and other memoirs.

Bütschli in his great work on the Protozoa ([1], p. 807) advanced the theory of the euglenoid ancestry. Given a typical Flagellate which became adapted first to a saprophytic, and then to a parasitic mode of life, it would tend as the result of parasitism to become simplified in characters and to lose all special organs of locomotion, nutrition, and sensation. An *Euglena* or *Astasia*, deprived in this way of flagellum, mouth, chromatophores, stigma, and vacuoles, nutritive or contractile, would be practically indistinguishable from a simple Gregarine. Considered generally, the body-form, cuticle, and contractile elements of the Gregarines are very similar to those of the typical Flagellata, and the resemblance of the "euglenoid" movements of Gregarines to those of "metabolic" Flagellata has already been pointed out. The same is true also of the motile stages of other Telosporidia; for example, the sporozoites and merozoites of the Coccidia, the oökinete or "vermiculus" of the malarial parasites, and the free haemogregarines of the Haemosporea. Since Bütschli wrote, the discovery of flagellated stages in many Telosporidia has given additional support to the Flagellate theory, and has caused Wasielewski to pronounce in favour of it.

The theory of the euglenoid ancestry of the Sporozoa is, in fact, based chiefly on certain characteristic features peculiar to the Gregarinida and other Telosporidia; but when the attempt is made to extend this hypothesis to the Neosporidia, the case is very different. It must be admitted at once that the Neosporidia have no euglenoid phases, and that the general facies of the group is strongly Rhizopod-like, as pointed out by Doflein [100] and other investigators. No Neosporidia are known to have flagella at any period of their life-cycle, and, with the possible exception of the gymnospores of Sarcosporidia, none of their phases are euglenoid or gregariniform. On the other hand, many of them are amoeboid, and have the protoplasm naked, without any sort of cuticle or envelope at the surface of the body, throughout the whole trophic period. Typical Myxosporidia can, in fact, be regarded as Rhizopods adapted to a parasitic mode of life. In their general features, especially in the formation of the pseudopodia, the structure and relations of the nuclei, and the alternation of generations, they resemble, as Doflein remarks, the Foraminifera most nearly, an indication, perhaps, of a common origin for the two groups. The adaptive modifications induced by the parasitism are shown chiefly, as in other parasites, in the increased fertility and elaboration of the reproductive phases, the differentiation of the spores, and so forth, points in which some forms are more advanced than others, but in which all are highly specialised, as compared with free-living Rhizopods.

Thus if the Telosporidia seem at first sight to afford some support to the theory of descent from Flagellate ancestors, the Neosporidia certainly do not, but exhibit most pronounced Rhizopod affinities. There is, considered from this point of view, a marked difference between the two subdivisions of the Sporozoa, and those who are greatly impressed by the euglenoid features of Gregarines and their allies might be tempted to postulate an independent origin for each sub-class, and to derive the Telosporidia from Flagellate, the Neosporidia from Rhizopod ancestors. But even in the Telosporidia the evidence afforded by the amoeboid character of the endoglobular Haemosporidia points very clearly to Rhizopod ancestry, and the euglenoid phases of this sub-class can be explained as derived from the primitive amoeboid type of body in just the same way as the higher "metabolic" forms of Flagellata, such as *Euglena* or *Astasia*, are related to primitive amoeboid types, such as *Mastigamoeba*.

The conclusion is, therefore, that in the present state of our knowledge it is simplest to regard all Sporozoa as descendants of Rhizopod-like ancestors, modified by the parasitism to which they are adapted. One immediate result of the changed conditions of life is that they can dispense with all special organs for ingesting or digesting food, since their nutriment is absorbed at the surface of the body. Hence many Sporozoa have acquired a permeable cuticle, and in consequence a fixed body-form. Such Flagellate characteristics as Sporozoa possess, for example the flagellated gametes of many Telosporidia, are found also among true Rhizopoda. To complete the argument in favour of Rhizopod ancestry, attention may be drawn finally to the remarkable parasitic amoebae described by Schewiakoff (*supra*, p. 318), which, if they are really allied to the Sporozoa, seem to prove quite conclusively the Rhizopod affinities of the group.

# LIST OF SPOROZOAN HOSTS.

The following list is taken mainly from Labbé [4], with additions and corrections from works of more recent date:—

## PROTOZOA.

| | | |
|---|---|---|
| *Ceratium macroceros* | .. | Sporozoön *inc. sed.* [L. Pfeiffer, 1895]. |
| *C. tripos* and *C. fusus* | ... | *Hyalosaccus ceratii*, Keppène. |
| *Ceratocorys horrida* | ... | ,, ,, |
| *Chlamydomonas* sp. | ... | Sporozoön, *inc. sed.* [L. Pfeiffer, 1895]. |
| Gregarines, various, especially *Sycia inopinata*, *Monocystis mitis*, *Selenidium spionis*, etc. | ... | *Metchnikovella* sp., Caull. et Mesn. |
| *Peridinium bipes* | ... | Sporozoön *inc. sed.* [L. Pfeiffer, 1895]. |
| *P. divergens* | ... | *Hyalosaccus ceratii*, Keppène. |
| *Stentor roeseli* | ... | Sporozoön *inc. sed.* [Stein, 1867. |
| *Stylobryon petiolatum* | ... | Sporozoön *inc. sed.* [Saville Kent, 1882]. |
| *Stylorhynchus longicollis* | ... | *Chytridiopsis socius*, Aim. Schn. |
| *Volvox globator* | ... | Sporozoön *inc. sed.* [Fromentel, 1874]. |

## CNIDARIA.

| | | |
|---|---|---|
| *Epizoanthus glacialis* | Ovarian cells | "Gregarine" [Danielssen, 1890]. |
| *Lucernaria auricula* | ... | "*Psorospermium*" *lucernariae* [Vallentin, 1888]. |

## ECHINODERMA.

| | | |
|---|---|---|
| *Chiridota pellucida* | Blood-vessels and coelom | *Cystobia holothuriae* (Ant. Schn.). |
| *Cucumaria pentactes* and *C. planci* | Respiratory trees and coelom | *C.* sp. [*fide* H. M. Woodcock in M.S.]. |
| *Echinocardium cordatum* and *E. flavescens* | Coelom | *Lithocystis schneideri*, Giard. |
| *Holothuria impatiens* | Blood-vessels and coelom | *Cystobia schneideri*, Ming. |
| *H. nigra* (=*H. forskalii*?) | Blood-vessels | *C. irregularis* (Minchin). |
| *H. polii* | Blood-vessels and coelom | *C. schneideri*, Ming. |
| *H. tubulosa* | ,, | *C. holothuriae* (Ant. Schn.). |
| *Spatangus purpureus* | Coelom | *Lithocystis schneideri*, Giard. |
| *Strongylocentrotus lividus* | ,, | (?) *Lithocystis schneideri*, Giard. |
| *Synapta digitata* and *S. inhaerens* | ,, | *Urospora synaptae* (Cuénot). |

### PLATYHELMINTHES.

| | | |
|---|---|---|
| *Brachycoelium* sp. | Parenchyma | *Pleistophora* sp. [Léger, 1897]. |
| *Convoluta* sp. | Gut (?) | *Urospora nemertis* (Köll.). |
| *Dendrocoelum lacteum* | ,, | "Gregarine" and "Coccidie" [Hallez, 1900] |
| *Discocoelis tigrina* | ,, | *Ophioidina discocoelidis*, Ming. |
| *Mesostomum ehrenbergi* | Testes and rhabdite-cells | Sporozoön *inc. sed.* [Ant. Schneider, 1873]. |
| *Planaria fusca* and *P. torva* | Gut | *Pleurozyga planariae*, Ming. |
| *Taenia bacillaris*, *T. denticulata*, and *T. expansa* | Parenchyma, gonads, ova | *Pleistophora helminthophthora* (Kef.). |

### NEMERTINI.

| | | |
|---|---|---|
| *Amphiporus cruciatus* | Gut | *Urospora nemertis* (Köll.). |
| *Borlasia olivacea* and *B. octoculata*; see *Lineus gesserensis*. | ... | |
| *Carinella annulata* | Body-cavity | "Monocystid Gregarine" [Montgomery, 1898]. |
| *Eupolia delineata* | Gut | *Urospora nemertis* (Köll.). |
| *Lineus gesserensis* | ,, | ,, ,, |
| ,, ,, | Posterior intestine | "Gregarine" [Montgomery, 1898]. |
| *Nemertes delineatus*; see *Eupolia*. | | |
| *Ommatoplea* sp. | Gut | *Urospora nemertis* (Köll.). |
| *Valencinia* sp. | ,, | ,, ,, |

### NEMATHELMINTHES.

| | | |
|---|---|---|
| *Ascaris lumbricoides* | ... | "*Gregarina*" sp. [Küchenmeister, 1855]. |
| *A. mystax* | Gut, gonads | *Pleistophora helminthophthora* (Kef.). |
| *Echinorhynchus proteus* | ... | "*Gregarina*" sp. [Henneguy, 1884]. |
| *Oxyuris ornata* | Body-cavity | "*G.*" sp. [Walter, 1858]. |

### CHAETOGNATHA.

| | | |
|---|---|---|
| *Sagitta claparedii* | Body-cavity | "*Amoeba*" *pigmentifera* Grassi, and "*A.*" *sagittae* Grassi. |
| *S.* sp. | Gut | *Lankesteria leuckarti* (Ming.). |
| *Spadella bipunctata* and *S. serratodentata* | Body-cavity | "*Amoeba*" *pigmentifera*, Grassi, and "*A.*" *sagittae*, Grassi. |

### ROTIFERA.

| | | |
|---|---|---|
| *Actinurus neptunius* | ... | *Glugea* sp. (? *Bertramia*) [Fritsch, 1895]. |
| *Asplanchna priodonta* and *A.* sp. | Body-cavity | *Bertramia asperospora* (Fritsch). |
| *Brachionus amphiceros*, *B. oön*, *B. pala*, and *B. urceolaris* | ,, | ,, ,, |

| | | |
|---|---|---|
| *Callidina parasitica* | Body-cavity | *Botellus* (?) sp. [Plate, 1886]. |
| *Conochilus volvox* | ,, | *Bertramia asperospora* (Fritsch). |
| *Hydatina senta* | Stomach | "*Monocystis*" *leydigi* [Stein, 1867]. |
| ,, ,, | Gut | *Botellus* (?) sp. [Lenssen, 1897]. |
| *Philodinid* sp. | Body-cavity | *Bertramia asperospora* (Fritsch). |
| *Polyarthra platyptera* | ,, | ,, ,, |
| *Synchaeta pectinata*, *S. tremula*, and *S.* sp. | ,, | ,, ,, |

### ARCHIANNELIDA.

| | | |
|---|---|---|
| *Ctenodrilus serratus* | Gut | *Selenidium* sp. (perhaps *echinatum*), C. & M. |
| *Polygordius neapolitanus* | ,, | "*Monocystis*" *foliacea* [Fraipont, 1887]. |

### POLYCHAETA.

| | | |
|---|---|---|
| *Alciope* sp. | Coelom | *Lobianchella beloneides*, Ming. |
| *Amphiglene mediterranea* | Coelom, intestine | *Toxosporidium sabellidarum*, C. & M. |
| *Aphrodite aculeata* | Gut | *Doliocystis aphroditae* (Lank.). |
| *Aricia latreilli* | ,, | *Siedleckia nematoides*, C. & M. |
| *A. mülleri*; see *Scoloplos.* | | |
| *A.* sp. | ,, | *Selenidium sabellae* (Lank.). |
| *Audouinia filigera* | ,, | *S. cirrhatuli* (Lank.). |
| ,, ,, | ,, | *Ulivina elliptica*, Ming. |
| ,, ,, | ,, | *Urospora nemertis* (Köll.). |
| *A. lamarcki* | ,, | *Gonospora terebellae* (Köll.). |
| *A.* sp. | Coelom | *G. varia*, Léger. |
| ,, | Gut | *Sycia inopinata*, Léger. |
| *A. tentaculata* | ,, | *Selenidium* sp., C. & M. |
| *Capitella capitata* | ,, | *Ancora sagittata* (Leuck.). |
| ,, ,, | Coelom | *Bertramia capitellae*, C. & M. |
| ,, ,, | Gut | "Coccidies" [Caullery & Mesnil, 1897]. |
| *Capitellides giardi* | ,, | "Gregarine" [Caullery & Mesnil, 1897]. |
| *Cirrhatulus cirratus* | ,, | *Selenidium cirrhatuli* (Lank.). |
| *C. filigerus*; see *Audouinia.* | | |
| *Clymene lumbricalis* | Coelom | *Pterospora maldaneorum*, Rac. & Labbé. |
| *Clymenella torquata* | ,, | "*Monocystis*" *clymenellae*, Porter. |
| *Dodecaceria concharum* | Gut | *Selenidium echinatum*, C. & M. |
| ,, ,, | Coelom | *Gonospora longissima*, C. & M. |
| *Eulalia punctifera* | ,, | *Urospora* sp., Gravier. |
| *Eunice harassei* | Gut | *Selenidium eunicae* (Lank.). |
| *Fabricia sabella* | Coelom, intestine | *Toxosporidium sabellidarum*, C. & M. |
| *Glycera* sp. | Coelom | *Ceratospora mirabilis*, Léger. |
| ,, | ,, | *Gonospora sparsa*, Léger. |
| *Heterocirrus viridis* | Gut | *Haplosporidium heterocirri*, C. & M. |
| *Jasmineira elegans* | Coelom, intestine | *Toxosporidium sabellidarum*, C. & M. |

| | | |
|---|---|---|
| *Lagis koreni* | Gut | *Joyeuxella toxoides*, Brasil. |
| *Liocephalus liopygus* | Coelom | *Pterospora maldaneorum*, Racov. & Labbé. |
| *Lumbriconereis* sp. | Gut | *Doliocystis elongata* (Ming.). |
| *Myxicola dinardensis* | Coelom, intestine | *Toxosporidium sabellidarum*, C. & M. |
| *Nephthys scolopendroides* | Gut | *Doliocystis heterocephala* (Ming.). |
| *Nereis beaucoudrayi* and *N. cultrifera* | ,, | *D. pellucida* (Köll.). |
| *Nerine* sp. | ,, | *Selenidium pendula*, Giard. |
| *Notomastus lineatus* | Intestine (?) | "Coccidies" [Caullery & Mesnil, 1899]. |
| *Oria armandi* | Coelom, intestine | *Toxosporidium sabellidarum*, C. & M. |
| *Phyllodoce* sp. | Coelom | *Gonospora sparsa*, Léger. |
| ,, | Gut | *Selenidium* sp. [Claparède, 1861]. |
| *Polydora agassizi* | ,, | *Doliocystis polydorae*, Léger. |
| *P. coeca* | ,, | *Selenidium* sp., C. & M. |
| *P. flava* | Intestine (?) | "Coccidies" [Caullery & Mesnil, 1897]. |
| *Polymnia nebulosa* | Testis | *Caryotropha mesnilii*, Siedl. |
| *Pomatoceros triqueter* | Gut | *Selenidium* sp., C. & M. |
| *Pygospio seticornis* | Intestine (?) | "Coccidies" [Caullery & Mesnil, 1899]. |
| ,, ,, | Gut | *Selenidium* sp., C. & M. |
| *Rhynchobolus americanus* | ... | "*Gregarina*" sp. [Porter, 1897]. |
| *Rhynchonerella fulgens* | Gut | *Selenidium annulatum* (Greeff.). |
| *Sabella* spp. | ,, | *Selenidium sabellae* (Lank.). |
| *Scololepis fuliginosa* | ,, | *Doliocystis* sp. |
| ,, ,, | ,, | *Selenidium* sp. |
| ,, ,, | Epidermis | *Glugea laverani*, C. & M. |
| *Scoloplos mülleri* | Gut | Coccidian sp. |
| ,, ,, | ,, | *Selenidium* sp. |
| ,, ,, | ,, | *Siedleckia nematoides*, C. & M. |
| ,, ,, | Coelom | *Haplosporidium scolopli*, C. & M. |
| ,, ,, | ,, | *Glugea laverani*, C. & M. |
| *Serpula contortuplicata* | Gut | *Selenidium serpulae* (Lank.). |
| *Spio fuliginosus* | ,, | *S. spionis* (Köll.). |
| *S. martinensis* | ,, | "Coccidies" [Caullery & Mesnil, 1899]. |
| ,, ,, | ,, | *Selenidium spionis* (Köll.). |
| *Staurocephalus rudolphii* | ,, | *Köllikerella staurocephali* (Ming.). |
| *Telepsavus costarum* | ,, | *Gonospora terebellae* (Köll.). |
| *Terebella* sp. | ,, | ,, ,, |

## OLIGOCHAETA.

| | | |
|---|---|---|
| *Allolobophora terrestris* | Vesiculae seminales | *Monocystis lumbrici* (Henle); *M. magna*, Schmidt; *M. pilosa*, Cuén.; and *M. porrecta*, Schmidt. |
| *Clitellio* sp. | ... | *Triactinomyxon ignotum*, Stolč. |
| *Distichopus silvestris* | Gut | *Monocystis mitis*, Leidy. |

| | | |
|---|---|---|
| *Eclipidrilus frigidus* | Blood-vessels and mesentery | *Haemogregarina nasuta* (Eisen). |
| ,, ,, | Vesiculae seminales | *Spermatophagus eclipidrili* (Eisen). |
| *Enchytraeus albidus*, *E. galba*, and *E. hegemon* | Vesiculae seminales and coelom | *Monocystis enchytraei*, Köll. |
| *Limnodrilus claparèdianus* | Coelom | *Myxocystis ciliata*, Mrázek. |
| *Lumbricus agricola* | Coelom and vesiculae seminales | *Zygocystis cometa*, Stein. |
| *L. herculeus*, *L. olidus*, *L. rubellus*, etc. | ,, | *Monocystis agilis*, Stein (= *lumbrici*, Henle); *M. magna*, Schmidt; *M. pilosa*, Cuén.; and *M. porrecta*, Schmidt. |
| *Megascolex armatus* | Vesiculae seminales | *M. perichaetae* (Bedd.). |
| *Nais lacustris* | ... | *Myxobolus* sp. [Bütschli, 1882]. |
| *Pachydrilus pagenstecheri*, *P. semifuscus* | Vesiculae seminales | *Monocystis pachydrili* (Clap.). |
| *Perichaeta armata;* see *Megascolex.* | | |
| *P. novaezealandiae.* | Coelom | "*Coccidium*" sp. [Beddard, 1888]. |
| ,, ,, | Seminal vesicles | *Monocystis perichaetae* (Beddard). |
| *Phoenicodrilus taste* | Vesiculae seminales | *Spermatophagus freundi* (Eisen). |
| *Phreatothrix pragensis* | ,, | Gregarine [Vejdovsky, 1876]. |
| *Psammoryctes barbatus* | ... | *Hexactinomyxon psammoryctis*, Stolč. |
| *Rhynchelmis obtusirostris* | Coelom | "*Monocystis*" sp. [Menge, 1845]. |
| *Tubifex rivulorum;* see *T. tubifex.* | | |
| *T. tubifex* | Vesiculae seminales and coelom | *Urospora saenuridis* (Köll.). |
| ,, ,, | ... | *Synactinomyxon tubificis*, Stolč. |

## Hirudinea.

| | | |
|---|---|---|
| *Glossiphonia complanata* (= *G. sexoculata*) | Coeca of gut | "*Gregarina*" sp. [Bolsius, 1895]. |
| *Haementeria officinalis* | Coelom and conjunctive tissue | ,, ,, |
| *Herpobdella atomaria* | Coeca of gut | ,, ,, |
| *Nephelis atomaria;* see *Herpobdella.* | | |
| *Piscicola geometra* | Haemocoele | ,, ,, |

## Gephyrea.

| | | |
|---|---|---|
| *Bonellia viridis* | Gut | *Ophioidina bonelliae* (Frnz.). |
| *Echiurus pallasi* | ,, | *Zygosoma gibbosum* (Greeff.). |
| *Sipunculus nudus* | Coelom | *Urospora sipunculi* (Köll.). |
| *Thalassema* sp. | ,, | *Monocystis thalassemae*, Lank. |

## Polyzoa.

| | | |
|---|---|---|
| *Alcyonellum fungosum* | Sperm-cells and body-cavity | *Glugea bryozoides* (Korotnef). |

## CRUSTACEA.

| | | |
|---|---|---|
| *Asellus aquaticus* | Ectoparasitic | *Amoebidium parasiticum*, Cienk. |
| *Astacus astacus* | Muscles | *Thélohania contejeani*, Henn. |
| ,, ,, | Intermuscular connective tissue | "*Psorospermium*" *haeckeli*, Hilgd. |
| *Balanus improvisus*, var. *gryphica* | Gut | "*Gregarina*" sp. [Solger, 1891]. |
| *B. perforatus* | ,, | *Nematoides fusiformis*, Ming. |
| *B. pusillus* and *B. tintinnabulum* | ,, | "*Gregarina*" *balani*, Köll. |
| *Cancer pagurus* | Gut and ovarian appendage | *Aggregata praemorsa* (Dies.). |
| *Candona candida* | Body-cavity | *Blanchardina cypricola* (Wrzski.). |
| ,, ,, | ,, | *Botellus parvus*, Monz. |
| *Canthocamptus minutus* | Gut | "*Monocystis*" *lacryma*, Vejd. |
| *Caprella* sp. | ,, | *Aggregata caprellae* (Frnz.). |
| *Carcinus maenas* | ,, | *A. portunidarum*, Frnz. |
| *Ceriodaphnia quadrangula* | Ectoparasitic | *Amoebidium moniezi*, Labbé. |
| ,, ,, | ... | *Pleistophora* sp. [Fritsch, 1895]. |
| *C. reticulata* | Ectoparasitic | *Amoebidium cienkowskianum*, Monz. |
| ,, ,, | Body-cavity | *Pleistophora obtusa* (Monz.). |
| ,, ,, | Gonads and haemocoele | *Botellus typicus*, Monz. |
| *Chydorus sphaericus* | Body-cavity | *Pleistophora obtusa* (Monz.). |
| ,, ,, | Body-cavity, gut, and dorsal organs | *Coelosporidium chydoricola*, Mesn. et March. |
| ,, ,, | Gonads and haemocoele | *Botellus typicus*, Monz. |
| *Crangon crangon* | Muscles | *Thélohania giardi*, Henn. |
| *Cyclops gigas* | Body-cavity and fat-body | *Pleistophora virgula* (Monz.). |
| *C. macrurus* | ... | "*Monocystis*" *mobilis* (Rehb.). |
| *C. phaleratus* | Body-cavity | Entoparasitic amoebae [Schewiakoff, 1894]. |
| *C. rubens;* see *Diaptomus* sp. | | |
| *C. strenuus* | ... | *Pleistophora rosea* (Fritsch). |
| *C.* sp. | Haemocoele and fat-body | (?) *P. obtusa* (Monz.). |
| ,, | ,, | *P. virgula* (Monz.). |
| ,, | Body-cavity | Entoparasitic amoebae [Schewiakoff, 1894]. |
| *Cypris candida;* see *Candona.* | | |
| *C. jurini;* see *C. strigata.* | | |
| *C. ophthalmica* | ,, | (?) *Botellus parvus*, Monz. |
| ,, | ... | *Pleistophora* sp. [Wierzejski, 1890]. |
| *C. ornata;* see *C. virens.* | | |
| *C. punctata;* see *C. ophthalmica.* | | |
| *C.* sp. | ... | *Pleistophora* sp. [Wierzejski, 1890]. |
| ,, | Body-cavity | *Serosporidium cypridis*, L. Pfr. |

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|---|---|---|
| *Cypris* sp. | Body-cavity | *Blanchardina cypricola* (Wrzski.). |
| *C. strigata* | ,, | *Serosporidium* sp., L. Pfr. |
| *C. vidua* | ... | *Pleistophora* sp. [Wierzejski, 1890]. |
| ,, | Body-cavity | *Botellus parvus*, Monz. |
| *C. virens* | ,, | *Serosporidium mülleri*, L. Pfr. |
| *Daphnia kahlbergiensis* | ... | *Pleistophora* sp. [Fritsch, 1895]. |
| *D. longispina* | Haemocoele | *P. obtusa* (Monz.). |
| *D. maxima* | Hypodermis | *Gurleya tetraspora*, Dofl. |
| *D. pulex* | ,, | *Pleistophora coccoidea* (L. Pfr.). |
| ,, | Body-cavity | *P. obtusa* (Monz.); *P.* (?) *virgula* (Monz.), and *Botellus daphniae* (L. Pfr.). |
| *D. rectirostris*; see *Moina*. | | |
| *D. reticulata*; see *Ceriodaphnia*. | | |
| *D. sima*; see *Simocephalus vetulus*. | | |
| *Diaptomus gracilis* | ... | *P. colorata* (Fritsch). |
| ,, ,, | Ectoparasitic on abdomen | *Amoebidium moniezi*, Labbé. |
| *D. salinus* | ... | *Pleistophora schmeili* (L. Pfr.). |
| *D.* sp. | ... | "*Monocystis*" *mobilis* (Rehb.). |
| ,, | Body-cavity | Entoparasitic amoebae [Schewiakoff, 1894]. |
| *D. vulgaris* | ... | *Pleistophora schmeili* (L. Pfr.). |
| *Dromia dromia* | Gut | *Aggregata dromiae* (Frnz.). |
| *Eurycercus lamellatus* | Ectoparasitic | *Amoebidium crassum*, Monz. |
| *Gammarus locusta* | Gut | Monocystid Gregarine [Original observation]. |
| *G. pulex* | ,, | *Didymophyes longissima*, Sieb. |
| ,, ,, | ,, | "*Gregarina*" sp. [L. Pfeiffer, 1895]. |
| ,, ,, | Muscles | *Thélohania mülleri* (L. Pfr.). |
| ,, ,, | Body-cavity | *Serosporidium gammari*, L. Pfr. |
| ,, ,, | Ectoparasitic | *Amoebidium parasiticum*, Cienk. |
| *G. puteanus*; see *Niphargus subterraneus*. | | |
| *Heterocope* sp. | ... | *Pleistophora* sp. [Frič and Vávra, in Pfeiffer, 1892]. |
| *Holopedium gibberum* | Heart, haemocoele, gut | *P. holopedii* (Frič and Vávra). |
| *Homarus gammarus* | Gut | *Porospora gigantea* (v. Ben.). |
| *Hyale pontica* | ,, | *Aggregata nicaeae* (Frnz.). |
| *Lathonura rectirostris* | Ectoparasitic | *Amoebidium cienkowskianum*, Monz. |
| *Limnetis* sp. | Hypodermic cells | *Pleistophora coccoidea* (L. Pfr.). |
| *Lynceus sphaericus*; see *Chydorus*. | | |
| *Moina rectirostris* | Body-cavity | *Pleistophora obtusa* (Monz). |
| ,, ,, | Gonads and haemocoele | *Botellus typicus*, Monz. |
| *Nebalia serrata* | Gut | Septate Gregarine [Original observation]. |
| *Nicaea nilsoni*; see *Hyale pontica*. | | |

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|---|---|---|
| *Niphargus subterraneus* | Gut | *Zygocystis puteana*, Lachm. |
| *Notodromas monacha* | Body-cavity | *Blanchardina cypricola* (Wrzski.). |
| *Orchestia littorea* | Gut | (?) *Didymophyes longissima*, Sieb. |
| *Pachygrapsus marmoratus* | ,, | *Aggregata conformis* (Dies.). |
| *Palaemon aspersus* and *P. serratus* | Muscles | *Thélohania octospora*, Henn. |
| *P. rectirostris*; see *P. aspersus*. | | |
| *Palaemonetcs varians* | ,, | *T. macrocystis*, Gurley. |
| *Paradoxostoma* sp. | Shell and body | *Pleistophora* sp. [G. W. Müller, 1894]. |
| *Pasithea rectirostris*; see *Lathonura*. | | |
| *Phronima sedentaria* | Stomach | *Callyntrochlamys phronimae*, Frnz. |
| *P.* sp. | Gut | "*Gregarina*" *clausi*, Frnz. |
| *Phronimella* sp. | ,, | ,, ,, |
| *Pinnotheres pisum* | Body-cavity | *Aggregata coelomica*, Léger. |
| *Pollicipes cornucopia* | Gut | *Nematoides fusiformis*, Ming. |
| *P. polymerus* | ,, | "*Gregarina*" *valettei*, Nussbaum. |
| *Polyphemus* sp. | Body-cavity | *Pleistophora obtusa* (Monz.). |
| *Portunus arcuatus* | Gut | *Aggregata portunidarum*, Frnz. |
| ,, ,, | ,, | *Zygocystis portuni* (Frnz.). |
| *Sapphirina* sp. | ,, | *Ophioidina haeckeli*, Ming. |
| *Simocephalus vetulus* | Ectoparasitic | *Amoebidium cienkowskianum*, Monz. |
| ,, ,, | Body-cavity | *Pleistophora obtusa* (Monz.). |
| *Typton spongicola* | Gut | *Callyntrochlamys* sp. [Gabriel, 1880]. |

## ONYCHOPHORA.

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|---|---|---|
| *Peripatus capensis* | Gut | *Gregarina* sp. [Moseley, 1874]. |

## MYRIAPODA.

| | | |
|---|---|---|
| *Cryptops hortensis* | Gut | *Dactylophorus robustus* (Léger). |
| *C. punctatus* | ,, | *Klossia bigemina* (Labbé). |
| *C.* sp. | ,, | "*Eimeria*" *trigemina* [Léger, 1897]. |
| *Fontaria virginiensis* | ,, | "*Gregarina*" *polydesmivirginiensis*, Leidy. |
| *Geophilus ferruginosus* | ,, | *Coccidium pfeifferi* (Labbé). |
| *G.* sp. | ,, | *Rhopalonia geophili*, Léger; *Coccidium* sp. [Léger, 1897]; *Cyclospora* sp. [Léger, 1896]. |
| *Glomeris guttata* and *G. ornata* | Malpighian tubes | *Légerella nova* (Aim. Schn.). |
| *G. marginata* | Testis | *L. testiculi*, Cuén. |
| *G.* sp. | Gut | *Cnemidospora lutea*, Aim. Schn.; *Cyclospora glomericola*, Aim. Schn. |
| *Himantarium gabrielis* | ,, | *Coccidium simondi* (Léger). |
| *Julus marginatus*; see *Spirobolus*. | | |

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| *Julus pusillus* | Gut | "*Gregarina*" *julipusilli*, Leidy. |
| *J. sabulosus* and *J. terrestris* | ,, | *Stenophora juli* (Frantz). |
| *Lithobius castaneus* | ,, | *Coccidium simondi* (Léger). |
| *L. forficatus* | ,, | *Actinocephalus dujardini*, Aim. Schn. |
| ,, ,, | ,, | *Echinomera hispida*, Aim. Schn. |
| ,, ,, | ,, | *Adelea ovata*, Aim. Schn. |
| ,, ,, | ,, | *Barroussia alpina*, Lég. |
| ,, ,, | ,, | *Coccidium schubergi*, Schaud., and *C. lacazei* (=*Bananella lacazei*, Labbé + *Eimeria schneideri*, Bütschli). |
| *L. hexodus* | ,, | *Echinospora ventricosa*, Léger. |
| *L. impressus* | ,, | *Barroussia schneideri*, Léger. |
| *L. martini* | ,, | *B. caudata*, Léger. |
| *L. mutabilis* and *L. pyrenaicus* | ,, | *Echinospora labbéi*, Léger. |
| *L. pilicornis* | ,, | *Coccidium simondi* (Léger). |
| *Polydesmus complanatus* | ,, | *Amphoroides polydesmi* (Léger). |
| *P.* sp. | ,, | *Diaspora hydatidea*, Léger. |
| *P. virginiensis ;* see *Fontaria.* | | |
| *Polyxenus lagurus* | ,, | Gregarine [Léger & Duboscq, 1900]. |
| *Scolopendra cingulata* | ,, | *Adelea dimidiata* (Aim. Schn.); *Pterocephalus nobilis*, Aim. Schn. |
| *S. morsitans* | ,, | *A. dimidiata* (Aim. Schn.). |
| *Scolopocryptops sexspinosus* | ,, | "*Gregarina*" *actinotus* [Leidy, 1889]. |
| *Scutigera forceps* | ,, | "*G.*" *megacephala*, Leidy. |
| *S.* sp. | ,, | *Trichorhynchus pulcher*, Aim. Schn. |
| *Spirobolus marginatus* | Proventriculus | *Stenophora juli* (Frantz). |
| *Stigmatogaster gracilis* | Gut | *Rhopalonia geophili*, Léger; *Coccidium hagenmülleri*, Léger. |

### HEXAPODA.

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|---|---|---|
| *Acheta abbreviata* (Orthopt.) | Proventriculus, body-cavity (?) | *Gregarina achetae-abbreviatae*, Leidy. |
| *Agrion puella*, larva (Neuropt.) | Gut | *Menospora polyacantha*, Lég. |
| *Akis acuminata* and *A. algeriana* (Coleopt.) | Malpighian tubes | *Ophryocystis francisi*, Aim. Schn. |
| *A.* sp. | Gut | *Sphaerorhynchus ophioides* (Aim. Schn.). |
| ,, | Fat-body | *Adelea akidium*, Léger. |
| *Amara cuprea* (Coleopt.) | Gut | *Gregarina amarae*, Frantz. |
| *Anopheles* spp. (Dipt.) | Stomach, haemocoele, salivary glands | *Laverania malariae*, Gr. et Fel.; *Plasmodium malariae* (Lav.); and *P. vivax* (Gr. et Fel.). |
| *Antherea pernyi*, larva (Lepidopt.) | ... | *Glugea* sp. [Balbiani, 1882]. |
| *Anthrenus museorum*, larva (Coleopt.) | Gut | *Pyxinia möbiuszi*, Lég. & Dub. |
| *Aphis arundinis ;* see *Hyalopterus.* | | |

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| *Aphodius nitidulus* and *A. prodromus* (Coleopt.) | Gut | *Didymophyes leuckarti*, W. St. Marshall. |
| *Apis mellifera* (Hymenopt.) | Muscles | *Glugea* sp. [Leydig, 1863]. |
| *Asida grisea* (Coleopt.) | Gut | *Stylorhynchus oblongatus* (Hamm.). |
| *A. servillei*. | ,, | *Eirmocystis asidae*, Léger. |
| *Attacus pernyi*; see *Antherea*. | | |
| *Attagenus pellio*, larva (Coleopt.) | ,, | *Pyxinia frenzeli*, L. & M. |
| *Bibio marci*, larva (Dipt.) | ,, | *Schneideria mucronata*, Lég. |
| *Blabera claraziana* (Orthopt.) | ,, | *Pileocephalus blaberae* (Frenzel). |
| *Blaps magica* (Coleopt.) | ,, | *Ophryocystis schneideri*, Léger. |
| *B. mortisaga* | ,, | *Stylorhynchus longicollis*, F. St. |
| ,, | Malpighian tubes | *Ophryocystis bütschlii*, Aim. Schn. |
| ,, | Epithelium of gut | *Chytridiopsis socius*, Aim. Schn. |
| *Bombyx mori*, larva (Lepidopt.) | All organs | *Glugea bombycis* (Nägeli). |
| *Brassolis astyra* (Lepidopt.) | Gut, Malpighian tubules, spinning glands, gonads | *G. astyrae* (Lutz & Splendore). |
| *Calliphora vomitoria* (Dipt.) | Head, thorax, blood (?) | "Pébrine" [Vosseler, 1897]. |
| *Calopteryx virgo*, larva (Neuropt.) | Gut | *Hoplorhynchus oligacanthus* (Sieb.). |
| *Carabus auratus* (Coleopt.) | ,, | *Actinocephalus stelliformis*, Aim. Schn.; *Ancyrophora gracilis*, Léger. |
| ,, ,, | Body-cavity | *Monocystis légeri*, L. F. Blanchard. |
| *C. glabratus* | Gut | *Actinocephalus acus*, Stein. |
| *C. violaceus* | ,, | *A. stelliformis*, Aim. Schn.; *Ancyrophora gracilis*, Léger. |
| *Catopsilia eubule* (Lepidopt.) | Gut, Malpighian tubules, spinning glands, gonads | *Glugea eubules* (Lutz & Splendore). |
| *Ceratopogon* sp., larva (Dipt.) | Gut | *Schizocystis gregarinoides*, Lég. |
| *Cetonia aurata* (Coleopt.). | ,, | *Gregarina curvata* (Hamm.). |
| *Chironomus* sp., larva (Dipt.) | ,, | *Schneideria* sp. [Léger, 1899]. |
| *Chlaenius vestitus* (Coleopt.) | ,, | *Actinocephalus digitatus*, Aim. Schn. |
| *Chrysomela haemoptera* and *C. violacea* (Coleopt.) | ,, | *Gregarina munieri* (Aim. Schn.). |
| *C. populi*; see *Melasoma*. | | ... |
| *Coecus hesperidum* (Homopt.) | ... | *Glugeidae* [Leydig, 1854]. |
| "*Coleoptère hydrocanthare*": | Gut | *Coccidium hyalinum*, Léger. |
| *Colymbetes* sp., larva (Coleopt.) | ,, | *Légeria agilis* (Aim. Schn).; *Ancyrophora uncinata*, Lég. |
| *Corynetes ruficollis*; see *Necrobia*. | | |
| *Ctenophora* sp., larva (Dipt.). | ,, | (?) *Actinocephalus* sp. [Léger, 1899]. |

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| *Culex* spp. (Dipt.) | Stomach, haemocoele, salivary glands | *Haemoproteus danilewskyi*, Kruse. |
| *Cyphon pallidus*, larva (Coleopt.) | Gut | *Sphaerocystis simplex*, Léger. |
| *Danais erippus* and *D. gilippus* (Lepidopt.) | Gut, Malpighian tubules, spinning glands, gonads | *Glugea erippi* [errore *grippi*] (Lutz & Splendore). |
| *Decticus griseus ;* see *Platycleis.* | | |
| *Dermestes lardarius* (Coleopt). | Gut | *Pyxinia rubecula*, Hamm. |
| *D. l.*, larva | ,, | *Beloides firmus* (Léger). |
| *D. peruvianus* | ,, | *Pyxinia crystalligera*, Frnz. |
| *D. undulatus*, larva | ,, | *Beloides tenuis* (Léger). |
| *D. vulgaris* (?) | ,, | *Pyxinia crystalligera*, Frnz. |
| *D. vulpinus* | ,, | *P. rubecula*, Hamm. |
| *Dione juno* (Lepidopt.) | Gut, Malpighian tubules, spinning glands, gonads | *Glugea junonis* (Lutz & Splendore). |
| *D. vanillae* | Gut ,, | *G. vanillae* (Lutz & Splendore). |
| *Dissosteira carolina* (Orthopt.) | ,, | *Gregarina locustaecarolinae* Leidy. |
| *Dorcus parallelepipedus* (Coleopt.) | ,, | *Stephanophora lucani* (F. St.). |
| *Dytiscus* sp., larva (Coleopt.) | ,, | *Ancyrophora uncinata*, Léger. |
| *Ectobia lapponica* (Orthopt.) | ,, | *Gamocystis tenax*, Aim. Schn. |
| *Ephemera* sp., larva (Neuropt.) | ,, | *Gregarina granulosa* (A. Schn.). |
| ,, ,, | ,, | *Gamocystis ephemerae* (Frantz). (= *G. francisci*, A. Schn.). |
| *Forficula auricularia* (Orthopt.) | ,, | *Gregarina ovata*, Duf. |
| *Gastropacha neustria*, larva (Lepidopt.) | All organs | *Glugea bombycis* (Nägeli). |
| *Geotrupes stercorarius* (Coleopt.) | Gut | *Didymophyes paradoxa*, F. St. |
| *Gryllotalpa gryllotalpa* (Orthopt.) | ,, | *Eirmocystis gryllotalpae*, Léger. |
| *G.* sp. | Midgut | *Glugea* sp. (Lutz & Splendore, 1903). |
| *Gryllus campestris* (Orthopt.) | ... | *G.* sp. (Vlacovitch, 1867). |
| *G. domesticus* | Gut | *Gregarina gryllorum*, Cuén., and *G. macrocephala* (A. Schn.) |
| ,, | Body-cavity | *Diplocystis major*, Cuén. ; and *D. minor*, Cuén. |
| *G.* sp. | Gut | *Gregarina davini*, Lég. & Dub. |
| *G. sylvestris ;* see *Nemobius.* | | |
| *Gyrinus natator*, larva (Coleopt.) | ,, | *Corycella armata*, Léger. |
| *G.* sp., larva | ,, | *Adelea simplex* (Aim. Schn.) ; "*Eimeria*" *hirsuta*, Aim. Schn. |
| *Helops striatus* (Coleopt.) | ,, | *Lophocephalus insignis* (Aim. Schn.). |
| *Hoplocephala bicornis* (Coleopt.) | ,, | *Gregarina microcephala* Leidy |

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| *Hyalopterus arundinis* (Homopt.) | Body-cavity and fat-body | *Neozygitis aphidis*, Witl. |
| *Hydaticus* sp. (Coleopt.) | Gut | *Bothriopsis histrio*, Aim. Schn. |
| *Hydrobius* sp., larva (Coleopt.) | ,, | *Cometoides crinitus* (Léger). |
| *Hydrophilus piceus* larva (Coleopt.) | ,, | *Phialoides ornata* (Léger). |
| *Hydrous caraboides*, larva (Coleopt.) | ,, | *Acanthospora polymorpha*, Léger. |
| *H.* sp. larva | ,, | *Cometoides capitatus* (Léger). |
| *Lecanium hesperidum* (Homopt.) | Body-cavity | Sporozoön *inc. sed.* [Leydig, 1853]. |
| *Lepisma saccharina* (Apt.) | Gut | *Gregarina lagenoides* (Léger). |
| *Libellulidae*, various, nymphs (Neuropt.) | ,, | *Geneiorhynchus monnieri*, A. Schn. |
| *Limnobia* sp., larva (Dipt.). | ,, | *Eirmocystis polymorpha*, Léger. |
| *Limnophilus rhombicus*, larva (Neuropt.) | ,, | *Ancyrophora uncinata*, Léger. |
| *Locusta carolina;* see *Dissosteira.* | | |
| *Lophocampa flavostica* (Lepidopt.) | Gut, Malpighian tubules, spinning glands, gonads | *Glugea lophocampae* (Lutz & Splendore). |
| *Lucanus parallelepipedus;* see *Dorcus.* | | |
| *Machilis cylindrica* (Apt.) | Gut | *Hyalospora affinis*, Aim. Schn. |
| *Mechanites lysimnia* (Lepidopt.) | Gut, Malpighian tubules, spinning glands, gonads | *Glugea lysimniae* (Lutz & Splendore). |
| *Melasoma populi* (Coleopt.) | Malpighian tubes | *G.* sp., L. Pfr. |
| *Melolontha brunnea* (?) (Coleopt.) | Gut | *Gregarina melolonthae-brunneae*, Leidy. |
| *M.* sp., larva | ,, | *Stictospora provincialis*, Léger. |
| *Morica* sp. (Coleopt.) | ,, | *Oocephalus hispanus*, Aim. Schn. |
| *Mystacides* sp. (Neuropt.) | ,, | *Gregarina mystacidarum* (Frantz). |
| *M.* sp., larva | ,, | *Pileocephalus chinensis*, Aim. Schn. |
| *Necrobia ruficollis* (Coleopt.) | ,, | *P. bergi* (Frnz.). |
| *Nemobius silvestris* (Orthopt.) | ,, | *Gregarina macrocephala*, A. Schn. |
| *Nepa cinerea* (Hemipt.) | ,, | *Coleorhynchus heros* (Aim. Schn.) |
| ,, ,, | Body-cavity and fat-body | *Syncystis mirabilis*, Aim. Schn. |
| ,, ,, | Gut | *Barroussia ornata*, Aim. Schn. (=*Eimeria nepae*, Aim. Schn.) |
| *Nyctobates pennsylvanica* (Coleopt.) | Proventriculus | *Gregarina philica*, Leidy. |
| *Ocypus olens* (Coleopt.) | Gut | *Actinocephalus stelliformis*, Aim. Schn. |
| ,, ,, | ... | "*Glugea*" sp. [Frey & Lebert, 1856]. |
| *Olocrates abbreviatus* (Coleopt.) | ... | *Adelea akidium*, Léger. |

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|---|---|---|
| *Olocrates gibbus* | Intestinal epithelium | *Rhaphidospora le danteci*, Léger. |
| ,, ,, | Malpighian tubes | *Ophryocystis hagenmülleri*, Léger. |
| *Omoplus* sp., larva (Coleopt.) | Gut | *Acanthospora pileata*, Léger. |
| *Opatrum sabulosum* (Coleopt.) | ,, | *Stylorhynchus oblongatus* (Hamm.). |
| *Orchesella villosa* (Apt.) | ,, | *Gregarina podurae* (Léger). |
| *Oryctes nasicornis*, larva (Coleopt.) | ,, | *Didymophyes gigantea*, F. St. |
| *Pachyrhina pratensis* (Dipt.) | ,, | *Eirmocystis ventricosa*, Lég. |
| ,, ,, | Fat-body, connective tissue, and muscles | *Glugea stricta* (Monz.). |
| *Pamphagus* sp. (Orthopt.) | Gut | *Gregarina acridiorum* (Léger). |
| *Panchlora exoleta* (Orthopt.) | ,, | *G. panchlorae*, Frenzel. |
| *Parnus* sp. (Coleopt.) | ,, | *G. laucournetensis* (Aim. Schn.). |
| *Passalus cornutus* (Coleopt.) | Proventriculus | *G. passalicornuti*, Leidy. |
| *Periplaneta americana* (Orthopt.) | Body-cavity | *Diplocystis schneideri*, Künstl. |
| ,, ,, | Gut and Malpighian tubules | *Glugea periplanetae* (Lutz and Splendore). |
| *P. orientalis* | Gut | *Gregarina blattarum* Sieb.; *G. blattaeorientalis*, Leidy. |
| ,, ,, | ... | *Glugeidae* [Schaudinn, 1902]. |
| *Petrobius maritimus* (?) (Coleopt.) | Gut | *Hyalospora roscoviana*, Aim. Schn. |
| *Phryganea grandis*, larva (Neuropt.) | ,, | *Asterophora elegans*, Lég. |
| *P. rhombica;* see *Limnophilus.* | | |
| *Phryganeidae*, larvae | Gut | *Pileocephalus heerii* (Köll.). |
| ,, ,, | Ectoparasitic | *Amoebidium parasiticum*, Cienk. |
| *Phyllognathus* sp. (Coleopt.) | Gut | *Didymophyes gigantea*, F. St. |
| *Phymata crassipes* (Hemipt.) | ,, | *Gregarina soror*, Duf. |
| Pierid sp. (Lepidopt.) | .... | *Glugea* sp. [Lutz and Splendore, 1903]. |
| *Pimelia* sp. (Coleopt.) | ,, | *Cystocephalus algerianus*, Aim. Schn. |
| *Platycleis grisea* (Orthopt.). | ... | *Glugea* sp. [Balbiani, 1882]. |
| *Podura aquatica* (Apt.) | Gonads | *G. thysanurae* (L. Pfr.). |
| *P. villosa;* see *Orchesella.* | | |
| *Poecilus cupreus;* see *Amara.* | | |
| *Porthesia chrysorrhoea* (Lepidopt.) | Mid-gut | *G.* sp. [Frenzel, 1885]. |
| *Potamanthus* sp., larva (Neuropt.) | Gonads, ova, and fat-body | (?) *G.* sp. [L. Pfeiffer, 1895]. |
| *Pyralis viridana;* see *Tortrix.* | | |
| *Reduvius personatus* (Hemipt.) | Gut | *Hyalospora reduvii* (Ramdohr). |
| *Rhizotrogus aestivus* (Coleopt.) | ,, | *Euspora fallax*, Aim. Schn. |
| *R.* sp., larva | ,, | *Stictospora provincialis*, Lég.; *Actinocephalus stelliformis*, Aim. Schn. |
| *Rhyacophila* sp., larva (Neuropt.) | ,, | *Asterophora mucronata*, Lég. |
| *Sarcophaga carnaria* (Dipt.) | Head, thorax, blood (?) | "*Pébrine*" [Vosseler, 1897]. |

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|---|---|---|
| *Scarabaeus relictus* (?), larva (Coleopt.) | Gut | *Gregarina scarabaeirelicti*, Leidy. |
| *Scaurus tristis* (Coleopt.) | Malpighian tubes | *Ophryocystis caulleryi*, Léger. |
| *Sciara nitidicollis*, larva (Dipt.) | Gut | *Schneideria caudata* (Sieb.). |
| *Sericostoma* sp. larva (Neuropt.) | ,, | *Discorhynchus truncatus* (Lég).; *Asterophora elegans*, Lég.; *Ancyrophora uncinata*, Lég. |
| *Silpha laevigata* (Coleopt.) | ,, | *Actinocephalus acutispora*, Léger. |
| *S. thoracica*, larva | ,, | *Ancyrophora gracilis*, Léger. |
| *Simulium ornatum*, larva (Dipt.) | ... | *Glugea varians*, Lég. |
| *Sminthurus* sp. (Apt.) | ... | (?) *Glugea thysanurae* (L. Pfr.). |
| *Sphingonotus* sp. (Orthopt.) | ,, | *Gregarina acridiorum* (Léger). |
| *Staphylinus olens*; see *Ocypus olens.* | | |
| *Statira unicolor* (Coleopt.) | ,, | *G. statirae*, Frnz. |
| ,, ,, | Malpighian tubes | *Glugea* sp. [Frenzel, 1892]. |
| *Tanypus* sp., larva (Dipt.) | Gut | *Stylocystis praecox*, Lég. |
| *Tenebrio molitor* (Coleopt.) | ,, | *Stylorhynchus ovalis*, Stein. |
| ,, ,, | Malpighian tubes | *Ophryocystis mesnili*, Léger. |
| *T. m.*, larva | Gut | *Gregarina polymorpha* (Hamm.); *G. cuneata*, Stein; *G. steini*, Berndt. |
| *Termes flavipes* (Neuropt.) | ,, | "*G.*" *termitis*, Leidy. |
| *Thanasimus formicarius*, larva (Coleopt.) | ,, | *G. longirostris* (Léger). |
| *Timarcha tenebricosa* (Coleopt.) | ,, | *G. munieri* (Aim. Schn.). |
| *Tineola biselliella* (Lepidopt.) | Body-cavity | *Adelea mesnili*, Perez. |
| *Tipula oleracea* (Dipt.) | Gut | *Eirmocystis ventricosa*, Lég. |
| *T.* sp., larva | ,, | *Gregarina longa* (Lég); *Actinocephalus tipulae*, Lég.; *Adelea tipulae*, Lég. |
| *T. pratensis*; see *Pachyrhina.* | | |
| *Tortrix viridana* (Lepidopt.) | Body-cavity | *Chloromyxum diploxys* (Gurley). |
| *Tridactylus variegatus* (Orthopt.) | Gut | *Gregarina hyalocephala*, Duf. |
| *Trox perlatus* (Coleopt.) | ,, | *G. acuta* (Léger). |
| *Truxalis* sp. (Orthopt.) | ,, | *G. acridiorum* (Léger). |
| *Vanessa urticae*, larva (Lepidopt.) | ... | (?) *Gymnospora nigra*, Monz. |
| *Vespa media* (Hymenopt.) | Malpighian tubes | *Glugea* sp. [L. Pfeiffer, 1895]. |
| *Zygaena filipendulae* (Lepidopt.) | Fat-body, connective tissue, and muscles | *G. stricta* (Monz.). |

## ARACHNIDA.

| | | |
|---|---|---|
| Acarine, marine | Ectoparasitic | *Exosporidium marinum*, Sand. |
| *Aranea diadema* (= *Epeira d.*) | Heart and trunk muscles | *Glugea* sp. [Leydig, 1885]. |
| *Boophilus bovis*; see *Rhipicephalus annulatus.* | | |
| *Dermacentor reticulatus* | ... | *Piroplasma canis* (P. et G. V.). |
| *Haemaphysalis leachi* | ... | ,, ,, |

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|---|---|---|
| *Hydrachnid* sp. | ... | *Glugea* sp. [Lutz & Splendore, 1903]. |
| *Phalangidae*, spp. | Gut | *Sciadophora fissidens* (Rössler); *Stylorhynchus caudatus*, Rössl. |
| *Phalangium cornutum* | ,, | *S. phalangii* (Léger); *Acanthospora repelini*, Léger. |
| *P. crassum* | ,, | *S. phalangii* (Léger). |
| *P. opilio* | ,, | *S. goronowitschi* (Johansen); *Anthorhynchus sophiae* (Aim. Schn.); *Acanthospora repelini*, Léger. |
| *Rhipicephalus annulatus* | ... | *Piroplasma bigeminum* (Sm. & K.). |

## MOLLUSCA.

| | | |
|---|---|---|
| *Chiton fascicularis* | Liver | *Minchinia chitonis* (Lank.). |
| *C.* sp | Mantle | *Chitonicium simplex* [Plate, 1901]. |
| *Donax* sp. | Kidney | *Hyaloklossia pelseneeri*, Léger. |
| *Eledone moschata* | Gut | *Eucoccidium octopianum* (Ai. Schn.); (*Benedenia octopiana*, see under *Octopus*). |
| *Helix arbustorum; H. fruticum; H. hispida; H. hortensis; H. nemoralis; H. umbrosa* | Kidney | *Klossia helicina*, Aim. Schn. |
| *H. hortensis* | ,, | *Pfeifferella* sp. [J. J. Clarke, 1895]. |
| *Limax cinereo-niger* | Kidney (?) | *Isospora rara*, Aim. Schn. |
| *Neretina fluviatilis* | Kidney | *Klossia soror*, Aim. Schn. |
| *Octopus vulgaris* | Gut | *Eucoccidium octopianum* (Ai. Schn.) = *Benedenia* seu *Légeria* (Blanchard), seu *Klossia* (Labbé), seu *Légerina* (Jacquemet), *octopiana*, with 10-12 sporozoites [Jacquemet, 1903; cp. Lühe, 1902]. |
| *Patella vulgata* | Liver | *Minchinia* sp. [Labbé, 1896]. |
| *Pterotrachea* sp. | Body-cavity | *Gregarina pterotracheae* (Stuart). |
| *Sepia officinalis* | Gut | *Eucoccidium eberthi* (Labbé) = *Benedenia* (A. Schn.) seu *Klossia* (Labbé), seu *Légeria* (Blanchard), seu *Légerina* (Jacquemet), *eberthi* (Labbé), seu *octopiana* (Ai. Schn.), with 3 or 4 sporozoites [Jacquemet, 1903; cp. Lühe, 1902]. |
| *Solen vagina* | Mantle | *Nematopsis* sp. [Aim. Schneider, 1892]. |
| *Succinea gigantea* (?); *S. pfeifferi; S. putris* | Kidney | *Klossia helicina*, Aim. Schn. |
| *S. pfeifferi* | ,, | *Pfeifferella* sp. [J. J. Clarke, 1895]. |
| *Tellina* sp. | ,, | *Hyaloklossia pelseneeri*, Léger. |
| *Trochus* sp. | Liver | *Minchinia* sp. [Labbé, 1896]. |

### ENTEROPNEUSTA.

| | | |
|---|---|---|
| *Balanoglossus kupfferi* | Hepatic region of gut | *Monocystis* sp. [Spengel, 1893]. |
| *Glandiceps hacksi* | Oesophagus and gut | Sporozoön [Spengel, 1893]. |
| *Ptychodera clavigera* | Hepatic region of gut | *Monocystis* sp. [Spengel, 1893]. |
| *P. sarniensis* | Oesophagus and intestine | Sporozoön [Spengel, 1893]. |

### TUNICATA.

| | | |
|---|---|---|
| *Amaroecium punctum* | Gut | *Lankesteria amaroecii* (Giard.). |
| *Ciona intestinalis* | Stomach and rectum | *L. ascidiae* (Lank.). |
| *Clavellina producta* | Gut | *Pleurozyga clavellinae* (Köll.). |
| *Diazona violacea* | ,, | *Lankesteria diazonae* (Ming.). |
| *Distaplia magnilarva* | ,, | *Pleurozyga distapliae*, Ming. |
| *Perophora annectens* | ... | "*Gregarina*" sp. [Ritter, 1893]. |
| *Phallusia mammillata* | ,, | *Pleurozyga phallusiae* (Köll.). |
| *Salpa aeruginosa* | ,, | "*Gregarina*" *ensiformis* [Bargoni, 1894]. |
| *S. confoederata*; *S. vagina* | ,, | "*G.*" *flava* [Roboz, 1886]. |
| *S. maxima* | ,, | "*G.*" *salpae* [Frenzel, 1885]. |

### CEPHALOCHORDA.

| | | |
|---|---|---|
| *Amphioxus lanceolatus* | Gut epithelium | *Lankesteria* sp. [Pollard, 1893]. |
| ,, ,, | Gill bars and subcutaneous tissue | *Branchiocystis amphioxi*, Burchardt. |

### PISCES.

| | | |
|---|---|---|
| *Abramis brama* | Gills | *Myxobolus exiguus*, Thél. |
| ,, ,, | Gall-bladder | *Sphaerospora masovica*, Cohn. |
| *Acanthias acanthias* (= *A. vulgaris*) | Gut | *Goussia lucida* (Labbé). |
| ,, ,, | Gall-bladder | *Chloromyxum leydigi*, Ming. |
| *Acerina cernua* | Gut | *Henneguya tenuis*, Vaney & Conte. |
| ,, ,, | Mesentery | *Pleistophora acerinae*, Van. & Conte. |
| ,, ,, | Muscles | *Leptotheca perlata* (Gurley); *Henneguya creplini* (Gurley). |
| *Alburnus alburnus* | Ovary | *Rhabdospora thélohani*, Laguesse. |
| ,, ,, | Gills | *Myxobolus oviformis*, Gurley; *M. obesus*, Gurley. |
| *A. mirandella* | Ovary | *Pleistophora mirandellae*, Vaney et Conte. |
| *Alosa*, see *Clupea pilchardus*. | | |
| *Amiurus melas* | Base of dorsal fins | *Henneguya linearis* (Gurley). |
| *Ammodytes tobianus* | Gut | *Rhabdospora thélohani*, Laguesse; *Goussia bigemina*, Labbé. |

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|---|---|---|
| *Anguilla vulgaris* | Gut | *Goussia variabilis* (Thél.). |
| *Aphredoderus sayanus* | Muscles | *Henneguya monura* (Gurley). |
| *Atherina hepsetus* | Gall-bladder | *Leptotheca hepseti*, Thél. |
| *Barbus barbus* (=*B. fluviatilis*) | Gills | *Myxobolus mülleri*, Bütsch. |
| ,, ,, | Spleen, intestine, ovary | *M. pfeifferi*, Thél. |
| *Belone acus* and *B. belone* [=*B. vulgaris*] | Gall-bladder | *Myxidium sphaericum*, Thél. |
| *Blennius montagui* | Blood | *Haemogregarina bigemina*, L. & M. |
| *B. ocellatus* | Gall-bladder | *Sphaeromyxa incurvata*, Dofl. |
| *B. pholis* | Kidney tubules | *Sphaerospora divergens*, Thél. |
| ,, | Gall-bladder | *Myxidium incurvatum*, Thél. |
| ,, | Blood | *Haemogregarina bigemina*, L. & M. |
| ,, | Muscles | *Pleistophora typicalis*, Gurley. |
| *Box boöps*; *B. salpa* | Gall-bladder | *Ceratomyxa pallida*, Thél. |
| *Callionymus lyra* | ,, | *Myxidium incurvatum*, Thél. |
| ,, ,, | Muscles | *Chloromyxum quadratum*, Thél.; *Glugea destruens*, Thél. |
| *Caranx trachurus*; see *Trachurus*. | | |
| *Carassius carassius* | Body-cavity | *Myxobolus* sp. [Gurley, 1894]. |
| *Cepola rubescens* | Gall-bladder | *Sphaeromyxa balbianii*, Thél. |
| ,, ,, | Liver | *Glugea ovoidea*, Thél. |
| *Chondrostoma nasus* | Tongue | "*Psorosperms*" [Leydig, 1851]. |
| *Clupea harengus* | Liver | *Goussia clupearum* (Thél.). |
| *C. pilchardus* | ,, | ,, ,, |
| ,, | Testis | *Coccidium sardinae*, Thél. |
| ,, | Gall-bladder | *Ceratomyxa truncata*, Thél. |
| ,, | Heart | *Glugea cordis*, Thel. |
| *Cobitis fossilis*; see *Misgurnus*. | | |
| *Conger conger* | Gall-bladder | "*Myxosporidium*" *congri* [Perugia, 1891]. |
| *Coregonus lavaretus* [=*C. fera*] | Gill epithelium | *Myxobolus sphaeralis*, Gurley. |
| ,, ,, | Intermuscular tissue | *M. zschokkei*, Gurley. |
| ,, ,, | ,, | *Henneguya kolesnikovi* (Gurley). |
| ,, ,, | Gills | *H.* sp. [Claparède, 1874]. |
| *Coris giofredi* | Gall-bladder | *Glugea marionis*, Thél. |
| *C. julis* | Muscles | *Chloromyxum quadratum*, Thél. |
| ,, | Gall-bladder | *Glugea marionis*, Thél. |
| ,, | Liver | *G. depressa*, Thél. |
| *Cottus bubalis* | Gut | *Goussia variabilis* (Thél.). |
| ,, | Muscles | *Pleistophora typicalis*, Gurley. |
| *C. scorpius* | ,, | ,, ,, |
| *Crenilabrus mediterraneus* and *C. pavo* | Gall-bladder | *Ceratomyxa inaequalis*, Dofl. |
| *C. melops* | Gut | *Goussia variabilis* (Thél.). |
| ,, | Kidney tubules | *Sphaerospora divergens*, Thél. |
| ,, | Gall-bladder | *Ceratomyxa arcuata*, Thél. |
| ,, | Eye | *Myxobolus mülleri*, Bütsch. |
| ,, | Body-cavity | *Glugea gigantea*, Thél. |
| *C.* sp. | Gut, liver, spleen, and pancreas | *Rhabdospora thélohani*, Laguesse. |

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|---|---|---|
| *Cyprinodon variegatus* | Subcutaneous connective tissue | *Myxobolus lintoni*, Gurley. |
| *Cyprinus carpio* | Kidney tubules, gills | *M. cyprini*, Dofl. ; *Hoferellus cyprini* (Dofl.) ; *Myxobolus dispar*, Thél. |
| ,, ,, | Gut | *Rhabdospora thélohani*, Laguesse. |
| *Engraulis encrasicholus* | Liver | *Goussia clupearum* (Thél.). |
| *Entelurus aequoreus ;* see *Nerophis.* | | |
| *Erimyzon sucetta* | Gills | *Myxobolus globosus*, Gurley. |
| ,, ,, | Skin | *M. oblongus*, Gurley. |
| *Esox lucius* | Urinary bladder | *Myxidium lieberkühnii*, Büts. |
| ,, ,, | Gills, muscles, eye | *Henneguya psorospermica*, Thél. |
| ,, ,, | Eggs | *H. p. oviperda* (Cohn). |
| ,, ,, | Gills | *H. p. lobosa* (Cohn) ; *H. p. anura* (Cohn). |
| ,, ,, | Intracellular tissue of eye-muscles, etc. | *H. schizura* (Gurley). |
| *Flesus passer* | Gut | *Glugea stephani* (Hagenmüller). |
| *Gadus pollachius* | Connective tissue of eye-muscles | *G. punctifera*, Thél. |
| *Galeus galeus* | Gall-bladder | *Ceratomyxa sphaerulosa*, Thél. |
| *Gasterosteus aculeatus* | Liver | *Coccidium gasterostei*, Thél. |
| ,, ,, | Skin tumours | "Myxosporidian" [G. W. Müller, 1895]. |
| *G. a.* and *G. pungitius* | Kidney tubules and connective tissue of ovary | *Sphaerospora elegans*, Thél. |
| ,, ,, | Kidney tubules and ovary | *Henneguya media*, Thél.; *H. brevis*, Thél. |
| ,, ,, | Subcutaneous connective tissue, cornea, ovary | *Glugea anomala*, Monz. (= *G. microspora*, Thél.). |
| *G. pungitius* | Muscles | *Pleistophora typicalis*, Gurley. |
| *G.* sp. | Kidney tubules | *Rhabdospora thélohani*, Laguesse. |
| *Girardinus* sp. | Skin, musculature, wall of intestine | *Glugea girardini* (Lutz & Splendore). |
| *Gobio gobio* (= *G. fluviatilis*) | Gut | *Coccidium metchnikovi*, Laveran. |
| ,, ,, | Fins, gills, kidney, spleen | *Myxobolus oviformis*, Thél. |
| *Gobius albus ;* see *Latrunculus.* | | |
| *G. fluviatilis* | Body-cavity | "*Psorosperms*" [Leydig, 1851]. |
| *G. minutus* | Connective tissue | *Glugea anomala*, Monz. (= *G. microspora*, Thél.) |
| ,, | Liver | *Goussia variabilis*, Labbé. |
| *G. paganellus* (= *G. bicolor*) | Gut | ,, ,, (Thél.). |
| *Hippocampus brevirostris* | Bile-ducts | *Sphaeromyxa sabrazesi*, L. & M. |
| *Hybognathus nuchalis* | Connective tissue of lower jaw | *Henneguya macrura* (Gurley). |
| *Julis giofredi ;* see *Coris.* | | |

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|---|---|---|
| *Labeo niloticus* | ... | *Myxobolus unicapsulatus*, Gurley. |
| *Labrus festivus* | Liver | *Goussia thélohani*, Labbé. |
| *L. turdus* | Gall-bladder | *Ceratomyxa linospora*, Dofl. |
| *Lamna cornubica* | Gut | *Pfeifferella gigantea* (Labbé); *Coccidium giganteum*, Labbé. |
| *Latrunculus albus* | Subcutaneous connective tissue | *Glugea anomala*, Monz. (=*G. microspora*, Thél.). |
| *Lepadogaster gouani* | Gut | *Goussia variabilis* (Thél.). |
| *Leptocephalus conger;* see *Conger.* | | |
| *Leuciscus cephalus* | Gall-bladder | *Chloromyxum fluviatile*, Thél. |
| ,, ,, | Fins and gulls | *Myxobolus mülleri*, Bütsch. |
| *L. erythrophthalmus* | Gills | *Myxosoma dujardini*, Thél. |
| ,, ,, | Muscles and spleen | *Myxobolus dispar*, Thél. |
| *L. funduloides* | Scales | *M. transovalis*, Gurley. |
| *L. phoxinus* | Ovary | *Rhabdospora thélohani*, Laguesse. |
| ,, | Kidney and ovary | *Myxidium histophilum*, Thél.; *Myxobolus mülleri*, Büts. |
| ,, | ... | *Glugea* sp. [L. Pfeiffer, 1895]. |
| *L. rutilus* | Gills | *Myxosoma dujardini*, Thél. |
| ,, | Operculum and pseudobranch | *Myxobolus cycloides*, Gurley. |
| ,, | Gills | *Henneguya* sp. [Borne, 1886]. |
| ,, | Heart | "Psorosperms" [Leydig, 1851]. |
| *Lophius budegassa* | Gall-bladder | *Ceratomyxa appendiculata*, Thél. |
| *L. piscatorius* | ,, | ,, ,, |
| ,, | Urinary bladder | *Myxoproteus ambiguus* (Thél.). |
| ,, | Spinal ganglia and cranial nerves | *Glugea lophii*, Dofl. |
| *Lota lota* (=*L. vulgaris*) | Urinary bladder | *Myxidium lieberkühnii*, Bütsch.; *Chloromyxum mucronatum*, Gurley. |
| ,, ,, | Kidney | *Myxobolus dipleurus*, Gurley. |
| *Lucioperca lucioperca* (=*L. sandra*) | Gill epithelium | *M.* sp. [J. Müller, 1841]. |
| ,, ,, | Gills | "Psorosperms" [Heckel & Kner, 1858]. |
| *Merluccius merluccius* (=*M. vulgaris*) | Gall-bladder | *Leptotheca elongata*, Thél.; *Ceratomyxa globulifera*, Thél. |
| ,, ,, | ... | *Myxobolus merluccii* (Perugia). |
| *Misgurnus fossilis* | Kidney | *M. piriformis*, Thél. |
| *Motella maculata* | Gut and pyloric coeca | *Crystallospora crystalloides* (Thél.). |
| ,, ,, | Gall-bladder | *Sphaeromyxa balbianii*, Thél. |
| *M. tricirrata* | Gut and pyloric coeca | *Crystallospora crystalloides* (Thél.); *Goussia motellae* (Labbé). |
| ,, | Gall-bladder | *Ceratomyxa arcuata*, Thél.; *Sphaeromyxa balbianii*, Thél. |
| ,, | Liver | *Glugea ovoidea*, Thél. |
| *Mugil auratus; M. capito; M. chelo* | Stomach, pyloric coeca, gills, spleen, kidney | *Myxobolus exiguus*, Thél. |

| | | |
|---|---|---|
| *Mugil* sp. | Glomeruli of kidney | *Sphaerospora rostrata*, Thél. |
| *Mustelus canis* | Gut | *Goussia lucida* (Labbé). |
| ,, ,, | Gall-bladder | *Ceratomyxa sphaerulosa*, Thél. |
| *M. laevis* | ,, | ,, ,, |
| *Nerophis aequoreus* | ,, | *Myxidium incurvatum*, Thél. |
| ,, ,, | Muscles | *Chloromyxum quadratum*, Thél. |
| ,, ,, | Connective tissue of dorsal fin | *Glugea acuta*, Thél. |
| *Notropis megalops* | Skin | Myxosporidian [Linton, 1891]. |
| *Pagellus centrodontus* | Gall-bladder | *Ceratomyxa arcuata*, var. *typica*, Thél. |
| *Perca fluviatilis* | Gut | *Rhabdospora thélohani*, Laguesse. |
| ,, ,, | Gills | *Henneguya psorospermica* (Cohn); *Myxobolus textus*, Cohn. |
| *Phoxinus funduloides* and *P. laevis*; see *Leuciscus*. | | |
| *Phycis phycis* (=*P. mediterranea*) | Gall-bladder | *Leptotheca polymorpha*, Labbé. |
| *Pimelodus blochi*; see *Piramutana*. | | |
| *P. clarias*; see *Synodontis*. | | |
| *P. sebae* | Gills | *Henneguya linearis* (Gurley). |
| *Piramutana blochi* | ,, | *Myxobolus inaequalis*, Gurley. |
| *Platystoma fasciatum* | Gill-chamber | *Henneguya linearis* (Gurley). |
| *Pleuronectes platessa* | Gut | "Sporozoön" [Johnstone, 1901] = *Glugea* sp. [*fide* H. M. Woodcock in M.S.]. |
| *Pseudoplatystoma*; see *Platystoma*. | | |
| *Raia alba*; see *R. undulata*. | | |
| *R. asterias* | Gall-bladder | *Myxidium giganteum*, Dofl. |
| *R. batis*; *R. clavata* | ,, | *Chloromyxum leydigi*, Ming. |
| *R. mosaica* | Blood | *Haemogregarina delagei*, L. & M. |
| *R. punctata* | ,, | ,, ,, |
| *R. undulata* | Gall-bladder | *Chloromyxum leydigi*, Ming. |
| *Rhamdia sebae*; see *Pimelodus*. | | |
| *Rhina squatina* | ,, | *Chloromyxum leydigi*, Ming. |
| *Salvelinus fontinalis* | Blood, muscles, gut, and lymph | *Lymphosporidium truttae*, Calkins. |
| *Scardinius erythrophthalmus*; see *Leuciscus*. | | |
| *Scomber scombrus* | Gut | *Goussia clupearum* (Thél.). |
| ,, ,, | Gall-bladder | *Leptotheca parva*, Thél. |
| ,, ,, | Kidney tubules | *L. renicola*, Thél. |
| ,, ,, | Gills | "Psorosperms" [Borne, 1886]. |
| *Scorpaena porcus* | Gall-bladder | *Ceratomyxa arcuata*, var. *scorpaenarum*, Labbé. |
| *S. scrofa* | ,, | ,, ,, |
| ,, | ,, | *Myxidium incurvatum*, Thél. |
| *S.* sp. | ,, | *Leptotheca agilis* (Thél.). |
| *Scyllium canicula* | ,, | *Chloromyxum leydigi*, Ming. |
| *S. catulus*; see *S. stellare*. | | |
| *S. stellare* | Gut | *Goussia lucida* (Labbé). |

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|---|---|---|
| *Solea vulgaris* | Blood | *Haemogregarina simondi*, L. & M. |
| *Sphyraena sphyraena* (= *S. vulgaris*) | Gut | "*Cretya*" *neapolitana*, Ming. |
| *Spinax spinax* (= *S. vulgaris*) | Gall-bladder | *Chloromyxum leydigi*, Ming. |
| *Squalius cephalus ;* see *Leuciscus* | | |
| *Squatina angelus ;* see *Rhina squatina*. | | |
| *Stizostethium lucioperca ;* see *Lucioperca.* | | |
| *Syngnathus acus* | ,, | *Myxidium incurvatum*, Thél. |
| ,, ,, | Muscles | *Chloromyxum quadratum*, Thél. |
| ,, ,, | Connective tissue of dorsal fin | *Glugea acuta*, Thél. |
| *Synodontis schall* | Gills | *Myxobolus inaequalis*, Gurley. |
| ,, ,, | Head | *Henneguya strongylura*, Gurl. |
| *Thymallus thymallus* (= *T. vulgaris*) | Neurilemma (?) | *Myxobolus pfeifferi*, Thél. |
| *Tinca tinca* (= *T. fluviatilis* and *T. vulgaris*) | Gill epithelium | *Rhabdospora thélohani*, Laguesse. |
| ,, ,, | Liver, kidney, spleen | *Goussia minuta* (Thél.). |
| ,, ,, | Gills, spleen, kidney | *Myxobolus piriformis*, Thél. |
| ,, ,, | Swim-bladder, gills, kidney, spleen, liver, cornea | *M. ellipsoides*, Thél. |
| *Torpedo narce ; T. torpedo* (= *T. marmorata*) | Gall-bladder | *Chloromyxum leydigi*, Ming. |
| *Trachinus draco* | ,, | *Ceratomyxa reticularis*, Thél. ; *Myxidium incurvatum*, Thél. |
| *Trachurus trachurus* | Liver | *Goussia cruciata* (Thél.). |
| ,, ,, | Muscles | *Chloromyxum quadratum* Thél. |
| *Trygon pastinaca* (= *T. vulgaris*) | Gall-bladder | *Leptotheca agilis*, Thélohan ; *Chloromyxum leydigi*, Ming. |

### AMPHIBIA.

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|---|---|---|
| *Batrachoseps attenuatus* | Erythrocytes | *Haemapium riedyi*, Eisen. |
| *Bufo lentiginosus* | Kidney | *Leptotheca ohlmacheri* (Gurley). |
| *B. marinus* (= *B. agua*) | Gall-bladder | *Cystodiscus immersus*, Lutz. |
| *B.* sp. | Gut | *Diplospora* sp. [Grassi, 1881]. |
| *Cystignathus ocellatus ;* see *Leptodactylus.* | | |
| *Hyla arborea* (= *H. viridis*) | Blood | *Cytamoeba* sp. [Grassi, 1882]. |
| *Leptodactylus ocellatus* | Gall-bladder | *Cystodiscus immersus*, Lutz. |
| *Molge cristata* | Gut | *Coccidium proprium* (Aim. Schn.). |
| ,, ,, | Gall-bladder | *Chloromyxum caudatum*, Thél. |
| *M. marmorata ; M. palmata ; M. vulgaris ; M.* sp. | Gut | *Coccidium proprium* (Aim. Schn.). |
| *Rana esculenta* | ,, | *C. ranarum* (Labbé) (incl. *Karyophagus ranarum*, Labbé, and *Molybdis entzi*, Pach. ?) ; *Paracoccidium prevoti*, L. & M. |

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|---|---|---|
| *Rana esculenta* | Kidney | *Diplospora lieberkühni* (Labbé); *Leptotheca ohlmacheri* (Gurley); *L. ranae*, Thél. |
| ,, ,, | Renal epithelium | *Karyamoeba renis*, G. Tos. |
| ,, ,, | Blood, spleen, bone-marrow, etc. | *Lankesterella ranarum*, Lank., and *L. monilis*, Labbé (incl. *Haemogregarina magna*, Gr. et Fel.; *Laverania ranarum*, Kruse; *Dactylosoma splendens*, Labbé; and *Cytamoeba bacterifera*, Labbé). |
| *R. temporaria* | Kidney | *Diplospora lieberkühni* (Labbé); *Leptotheca ohlmacheri* (Gurley); *L. ranae*, Thél. |
| ,, ,, | Muscles | *Pleistophora danilewskyi* (L. Pfr.). |
| ,, ,, | Skin | "Myxosporidian" [G. W. Müller, 1895]. |
| *Salamandra salamandra* (= *S. maculata*) | Gut | *Coccidium salamandrae* (Steinhaus) (incl. *Karyophagus salamandrae*, Steinh.). |
| ,, ,, | Spermatocyte nuclei | *Micrococcidium caryolyticum* [Drüner, 1894]. |
| *Triton* spp.; see *Molge*. | | |

## Reptilia

| | | |
|---|---|---|
| *Alligator mississipiensis* | Blood | *Haemogregarina crocodilinorum*, Börner. |
| *Ancistrodon piscivorus* | ,, | *H. mocassini*, Lav. |
| *Anguis fragilis* | Gut | *Coccidium railleti*, Léger. |
| *Bothrops* sp. | Blood | *Drepanidium serpentium*, Lutz. |
| *Bungarus fasciatus* | ,, | *Haemogregarina bungari* (Billet). |
| *Chalcides tridactylus* | Muscles | (?) *Pleistophora danilewskyi* (L. Pfr.). |
| *Chameleo vulgaris* | Gut | *Diplospora mesnili*, Sergent. |
| *Cistudo europaea*; see *Emys*. | | |
| *Clemmys elegans* | Blood | *Haemogregarina labbéi*, Börn. |
| *Coelopeltis lacertina* | Gut | *Diplospora laverani*, Hagenmüller. |
| *Coluber aesculapii* | Blood | *Haemogregarina* sp. [Börner, 1901]. |
| *C. carbonarius*; see *Zamenis gemonensis*. | | |
| *C. corais* | ,, | *Drepanidium serpentium*, Lutz. |
| *Coronella austriaca* | Gut | *Coccidium* sp. [Grassi, 1888]. |
| *C.* sp. | ,, | *Isospora* sp. [Grassi, 1881]. |
| *Crocodilus frontatus* | Blood | *Haemogregarina crocodilinorum*, Börner. |
| *C.* sp. | Gut | *Coccidium* sp. [Solger & Gabriel, 1876]. |
| *Crotalus confluentus* | Blood | *Haemogregarina crotali*, Lav. |
| *C.* sp. | ,, | *Drepanidium serpentium*, Lutz. |

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| *Cryptopus granosus ;* see *Emyda.* | | |
| *Damonia reevesii* | Gut (rectum) | *Coccidium mitrarium,* L. & M. |
| ,, ,, | Blood | *Haemogregarina stepanoviana,* L. & M. |
| ,, ,, | ,, | *H. rara,* L. & M. |
| *Drymobius biforsatus* | ,, | *Drepanidium serpentium,* Lutz. |
| *Emyda granosa* | Gut | *Coccidium légeri,* Simond. |
| *Emys orbicularis* (= *E. lutaria* and *E. europaea* | ,, | *C. delagei,* Labbé. |
| ,, ,, | Blood | *Haemogregarina stepanovi,* Danil. |
| ,, ,, | Kidney | *Myxidium danilewski,* Lav. |
| ,, ,, | Muscles | *Pleistophora danilewskyi* (L. Pfr.). |
| *E. tecta ;* see *Kachuga.* | | |
| *Eunectes murinus* | Blood | *Drepanidium serpentium,* Lutz. |
| *Gavialis gangeticus* | Spleen | *Coccidium kermoganti,* Simond. |
| ,, ,, | Blood | *Haemogregarina hankini,* Simond. |
| *Gongylus ocellatus* | Gut | *Diplospora camillerii,* Hagen. |
| *Herpetodryas carinata* | Blood | *Drepanidium serpentium.* |
| *Kachuga tectum* | ,, | *Haemogregarina mesnili,* Simond. |
| *Lacerta agilis ; L. muralis* | ,, | *H. lacazei* (Labbé) ; *Karyolysus lacertarum* (Danil.). |
| *L. muralis* | Ovary | *Coccidium lacertae* (Ming.). |
| *L. ocellata ; L. viridis ; L.* sp. | Blood | *Karyolysus lacertarum* (Danil.). |
| *L.* sp. | Gut (and kidney ?) | *Coccidium* sp. [Eimer, 1870]. |
| ,, | Muscles | (?) *Pleistophora danilewskyi,* (L. Pfr.). |
| ,, | Ova | "Myxosporidian" [Mingazzini, 1892]. |
| *Naja tripudians* | Blood | *Haemogregarina najae,* Lav. |
| *Philodryas olfersii* | ,, | *Drepanidium serpentium,* Lutz. |
| *Platemys* sp. | ,, | *Haemogregarina labbéi,* Börn. |
| *Platydactylus mauritanicus ;* see *Tarentola.* | | |
| *Python reticulatus* | ,, | *H. pythonis* (Billet) ; *H. colubri,* Börner. |
| *Rhadinaea merremii* | ,, | *Drepanidium serpentium,* Lutz. |
| *Seps chalcides ;* see *Chalcides.* | | |
| *Spilotes pullatus* | ,, | ,, ,, |
| *Tarentola mauritanica* | Muscular fibres | *Sarcocystis platydactyli,* Bertram. |
| ,, ,, | Blood | *Haemogregarina platydactyli,* Billet. |
| *Testudo ibera* | ,, | *Karyolysus* (?) sp. [Popovici, 1901]. |
| *T. marginata* | ,, | *Haemogregarina stepanovi,* Danil. |
| *Trionyx indicus* | ,, | *Haemamoeba metchnikovi,* Simond. |
| *T.* sp. | ,, | *Haemogregarina stepanovi,* Danil. |

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| *T. stellatus* | Blood | *H. billeti*, Simond. |
| *Tropidonotus stolatus* | ,, | *H. pythonis*, Börner. |
| *Xenodon neuviedii* | ,, | *Drepanidium serpentium*, Lutz. |
| *Zamenis gemonensis* (=*Z. viridiflavus*) | Vasa deferentia | *Coccidium colubri* (Ming.). |
| ,, ,, | ... | *Pleistophora heteroica* (Monz.). |
| *Z. hippocrepis* | Blood | *Haemogregarina zamenis*, Lav. |

### Aves.

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|---|---|---|
| *Acanthis cannabina* | Gut | *Diplospora lacazei*, Labbé. |
| *Actitis hypoleucus*; see *Totanus*. | | |
| *Agelaeus phoeniceus* | Blood | *Halteridium danilewskyi* (Gr. & Fel.); *Haemoproteus danilewskyi*, Kruse. |
| *Alauda arvensis* | Gut | *Coccidium avium* (Silv. & Riv.); *Diplospora lacazei*, Labbé. |
| ,, ,, | Blood | *Halteridium danilewskyi* (Gr. & Fel.); *Haemoproteus danilewskyi*, Kruse. |
| *Alcedo ispida* | Gut | *Diplospora lacazei*, Labbé. |
| *Anas boschas*; *A. clypeata* | Intermuscular connective tissue | *Sarcocystis rileyi* (Stiles). |
| *A. domestica* | Gut | *Coccidium avium* (Silvestr. & Rivolta). |
| *Anser domesticus* | ,, | ,, ,, |
| ,, ,, | Kidney tubules | *C. truncatum*, Raill. & Lucet). |
| *Apus apus*; see *Cypselus a.* | | |
| *Arenaria interpres* | Gut | *C. roscoviense*, Labbé. |
| *Asio otus* | Blood | *Haemoproteus danilewskyi*, Kruse. |
| *Athene noctua*; see *Carine* | | |
| *Bubo virginianus*; *B.* sp. | ,, | *Halteridium danilewskyi* (Gr. & Fel.). |
| *Budytes flavus* | Gut | *Diplospora lacazei*, Labbé. |
| *Buteo buteo* (=*B. vulgaris*) | Blood | *Halteridium danilewskyi* (Gr. & Fel.); *Haemoproteus danilewskyi*, Kruse. |
| *Calidris arenaria* | Gut | *Coccidium roscoviense*, Labbé. |
| *Cannabina linota*; see *Acanthis c.* | | |
| *Carduelis carduelis* (=*C. elegans*) | ,, | *C. avium* (Labbé); *Diplospora lacazei*, Labbé. |
| *Carine noctua* | Blood | *Halteridium danilewskyi* (Gr. & Fel.). |
| *Charadrius alexandrinus*; *C. dubius*; *C. pluvialis* | Gut | *Coccidium roscoviense*, Labbé. |
| *Chelidonaria urbica* (=*Chelidon u.*) | ,, | *Diplospora lacazei*, Labbé. |
| *Chloris chloris* | ,, | ,, ,, |
| *Chrysomitris spinus* | ,, | ,, ,, |
| *Circus aeruginosus* | Blood | *Haemoproteus danilewskyi*, Kruse. |
| *Clivicola riparia* | Gut | *Diplospora lacazei*, Labbé. |
| *Coccothraustes coccothraustes* (=*C. vulgaris*) | ,, | ,, ,, |

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| *Colaeus monedula* | Blood | *Haemoproteus danilewskyi*, Kruse. |
| *Columba domestica* | Gut | *Coccidium pfeifferi*, Labbé. |
| ,, ,, | Blood | *Halteridium danilewskyi* (Gr. & Fel.). |
| *C. livia* | ,, | *Haemoproteus danilewskyi*, Kruse ; *Halteridium danilewskyi* (Gr. & Fel.). |
| *Coracias garrula* | Gut | *Diplospora lacazei*, Labbé. |
| *Corvus cornix* | Blood | *Haemoproteus danilewskyi*, Kruse. |
| *C. cornix ; C. corone* | Gut | *Diplospora lacazei*, Labbé. |
| *C. americanus ; C. corax* | Blood | *Halteridium danilewskyi* (Gr. & Fel.). |
| *C. frugilegus* | ,, | *Haemoproteus danilewskyi*, Kruse. |
| *Cotyle riparia;* see *Clivicola.* | | |
| *Cuculus canorus* | Gut | *Diplospora lacazei*, Labbé. |
| *Cypselus apus* | ,, | ,, ,, |
| *Dendrocopus minor* | ,, | ,, ,, |
| *Emberiza citrinella* | ,, | ,, ,, |
| *E. miliaria* (=*E. projer*) | Blood | *Halteridium danilewskyi* (Gr. & Fel.). |
| *Erithacus luscinia ; E. phoenicurus ; E. rubeculus* | Gut | *Diplospora lacazei*, Labbé. |
| *Falco tinnunculus* | Blood | *Halteridium danilewskyi* (Gr. & Fel.) ; *Haemoproteus danilewskyi*, Kruse. |
| *Fringilla canaria ;* see *Serinus* | | |
| *F. carduelis ;* see *Carduelis.* | | |
| *F. coelebs* | Gut | *Diplospora lacazei*, Labbé. |
| ,, | Blood | *Halteridium danilewskyi* (Gr. & Fel.) ; *Haemoproteus danilewskyi*, Kruse. |
| *F. montifringilla* | Gut | *Diplospora lacazei*, Labbé. |
| *Galerita cristata* | ,, | ,, ,, |
| *Gallus domesticus* | ,, | *Coccidium avium* (Silvestr. & Rivolta). |
| ,, ,, | Ova | *Coccidium* sp. (?) [Podwyssozki, 1890]. |
| ,, ,, | Muscles and connective tissue | *Sarcocystis* sp. [Kühn, 1865 ; Stiles, 1894]. |
| *Garrulus glandarius* | Blood | *Halteridium danilewskyi* (Gr. & Fel.). |
| *Habia ludoviciana* | Intramuscular connective tissue | *Sarcocystis falcatula*, Stiles. |
| *Hirundo rustica* | Gut | *Diplospora lacazei*, Labbé. |
| *Iynx torquilla* | ,, | ,, ,, |
| *Lanius collurio* | ,, | ,, ,, |
| *L. excubitor* | Blood | *Haemoproteus danilewskyi*, Kruse. |
| *L. minor ; L. senator* (=*L. rufus*) | ,, | ,, ,, |
| *Ligurinus chloris;* see *Chloris.* | | |
| *Luscinia vera* and *L. phoenicurus ;* see *Erithacus.* | | |
| *Meleagris gallopavo* | Gut | *Coccidium avium* (Silv. & Riv.). |

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| *Melospiza fasciata ; M. georgiana* | Blood | *Halteridium danilewskyi* (Gr. & Fel.) ; *Haemoproteus danilewskyi*, Kruse. |
| *Milvus migrans* | ,, | *Haemoproteus danilewskyi* (Kruse). |
| *Monedula turrium ;* see *Colaeus m.* | | |
| *Motacilla alba* | Gut | *Diplospora lacazei*, Labbé ; *Coccidium roscoviense*, Labbé. |
| *Muscicapa atricapilla* | ,, | *Diplospora lacazei*, Labbé. |
| *Numenius phaeopus* | ,, | *Coccidium roscoviense*, Labbé. |
| *Oriolus oriolus* (=*O. galbula*) | ,, | *Diplospora lacazei*, Labbé. |
| *Otus vulgaris ;* see *Asio otus.* | | |
| *Padda oryzivora* | Blood | *Halteridium danilewski* (Gr. et Fel.). |
| *Pandion haliaëtus* | ,, | *Haemoproteus danilewskyi*, Kruse. |
| *Parula pitiayumi* | Muscles | *Sarcocystis* sp. [Barrows, 1883]. |
| ,, ,, | Pectoral muscles | ,, ,, |
| (?) *Parus caeruleus* (=*P. cyaneus*) | Gut | *Diplospora lacazei*, Labbé. |
| *P. major* | Blood | "*Haemamoeba*" sp. [Laveran, 1902]. |
| *Passer domesticus* | Gut | *Diplospora lacazei*, Labbé. |
| ,, ,, | Blood | *Halteridium danilewskyi* (Gr. & Fel.) ; *Haemoproteus danilewskyi*, Kruse. |
| *P. hispaniolensis ; P. montanus* | ,, | *Haemoproteus danilewskyi*, Kruse. |
| *P. montanus* | ,, | *Halteridium danilewskyi* (Gr. & Fel.). |
| *Pavo cristatus* | Gut | (?) *Coccidium avium* (Silv. & Riv.). |
| *Pernis apivorus* | Blood | *Haemoproteus danilewkyi*, Kruse. |
| *Phalacrocorax graculus* (= *P. cristatus*) | Gut | *Coccidium roscoviense*, Labbé. |
| *Phasianus colchicus ; P.* sp. | ,, | *C. avium* (Silv. & Rivolt.). |
| *Pica pica* (=*P. caudata*) | Blood | *Haemoproteus danilewskyi*, Kruse. |
| *Picus minor ;* see *Dendrocopus m.* | | |
| *Pluvialis apricarius ;* see *Charadrius pluvialis.* | | |
| *Pyrrhula europaea* ( = *P. vulgaris*) | Gut | *Diplospora lacazei*, Labbé. |
| *Rubecula familiaris ;* see *Erithacus r.* | | |
| *Saxicola oenanthe* | ,, | ,, ,, |
| *Serinus canarius* | ,, | ,, ,, |
| *Setophaga ruticilla* | Muscles | *Sarcocystis* sp. [Stiles, 1894]. |
| *Spatula clypeata ;* see *Anas.* | | |
| *Strepsilas interpres ;* see *Arenaria.* | | |
| *Strix flammea* | Blood | *Halteridium danilewskyi* (Gr. et Fl.). |
| *Sturnus vulgaris* | Gut | *Diplospora lacazei*, Labbé. |
| ,, ,, | Blood | *Halteridium danilewskyi* (Gr. et Fel.). |

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| *Sylvia atricapilla; S. hortensis* | Gut | *Diplospora lacazei*, Labbé. |
| *Syrnium aluco* | Blood and bone-marrow | *Halteridium danilewskyi* (Gr. et Fel.). |
| *Totanus hypoleucus; T. totanus* (= *T. calidris*) | Gut | *Coccidium roscoviense*, Labbé. |
| *Tringa alpina; T.* sp. | ,, | ,, ,, |
| *Turdus merula* | ,, | *Diplospora lacazei*, Labbé. |
| ,, ,, | Connective tissue | *Sarcocystis* sp. [Kühn, 1865]. |
| *Turtur turtur* (= *T. auritus*) | Gut | *Coccidium pfeifferi*, Labbé. |
| *Upupa epops* | ,, | *Diplospora lacazei*, Labbé. |

### MAMMALIA.

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|---|---|---|
| Apes | Blood | *Plasmodium kochi* (Laveran). |
| *Bos taurus* | Intestine, bladder | *Coccidium perforans*, var., Hess & Zschokke. |
| ,, | Liver and intestine | *C. perforans*, var., Zurn. |
| ,, | Muscles | *Sarcocystis* sp. [Hessling, 1853]. |
| ,, | Blood | *Piroplasma bigeminum* (Sm. et K.) = *Babesia bovis* (Babes). |
| *Bubalus* sp. | Muscles | *Sarcocystis* sp. [Jongh, 1885]. |
| *Canis familiaris* | Intestine | *Coccidium bigeminum*, var. *canis*, Raill. et Lucet. |
| ,, ,, | Lungs | *C.* sp. [Lienaux, 1891]. |
| ,, ,, | Muscles | *Sarcocystis* sp. [Krause, 1863]. |
| ,, ,, | Blood | *Piroplasma canis* (P. et G. V.). |
| *Capra hircus* | Intestine | *Coccidium perforans*, var., Hess & Zschokke. |
| ,, ,, | Muscles | *Sarcocystis* sp. [Jongh, 1885]. |
| *Cavia cobaya* | Gut | *Cyclospora caryolytica*, Schaud. |
| *Cervus capreolus* | Muscles | *Sarcocystis* sp. [Hessling, 1853]. |
| *Cricetus cricetus* | Gut | *Cyclospora caryolytica*, Schaud. |
| *Equus caballus* | Kidney | "*Eimeria*" sp. [Pachinger, 1886]. |
| ,, ,, | Intestine | *Coccidium perforans*, var., Hess & Zschokke. |
| ,, ,, | Submucosa of intestine | *Globidium leuckarti* [Flesch, 1884]; *Sarcocystis* sp. [Gerlach, 1866]. |
| ,, ,, | Blood | *Piroplasma equi*, Laveran. |
| *Felis domestica* | Intestine | *Coccidium bigeminum*, var. *cati*, Raill. et Lucet. |
| ,, ,, | Muscles | *Sarcocystis* sp. [Krause, 1863]. |
| *Lepus cuniculus* | Intestine | *Coccidium perforans*, Leuck. |
| ,, ,, | Liver | *C. cuniculi* (Riv.) = *C. oviforme*, Leuck, incl. *Pfeifferella princeps* (Labbé). |
| ,, ,, | Ovum | *C.* sp. [Pdwyssozky, 1892]. |
| ,, ,, | Muscles | *Sarcocystis* sp. [Manz, 1867]. |
| *L. timidus* | Intestine | *Coccidium perforans*, Leuck. |
| ,, | Muscles | *Sarcocystis* sp. [Hardenberg, 1865]. |
| *Macacus* sp. | ,, | *S.* sp. [Ratzel, 1868]. |
| *Macropus penicillatus*; see *Petrogale*. | | |

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| *Miniopterus schreibersi* . | Blood . . | *Polychromophilus melaniphorus*, Dionisi. |
| *Mus decumanus* . . . | Muscles . . | *Sarcocystis* sp. [Siebold, 1853]. |
| *Mus musculus* . . . | Intestine . . | *Coccidium falciforme* (Eimer) (incl. *Eimeria falciformis* (A. Schn.); *Pfeifferia schubergi*, Labbé, etc.). |
| ,, . . . | Kidney . . . | *Klossiella muris*, Smith et Johnston. |
| ,, . . . | Muscles . . | *Sarcocystis muris* (Blanchard). |
| *M. rattus* . . . . . | ,, . . | *S.* sp. [Siebold, 1853]. |
| *Mustela putorius* . . | Intestine . . | *Coccidium bigeminum*, var. *putorii*, Raill. et Lucet. |
| *M. vulgaris* . . . | Gut . . . | *Cyclospora caryolytica*, Schaud. |
| *Myotis capaccinii* . . | Blood . . . | *Polychromophilus melanipherus*, Dionisi. |
| *M. myotis;* see *Vespertilio murinus.* | | |
| *Otaria californica;* see *Zalophus.* | | |
| *Ovis aries* . . . . | Intestine . . | *Coccidium perforans*, var., Curtice. |
| ,, . . . . | Muscles and connective tissue | *Sarcocystis tenella*, Raill. |
| ,, . . . . | Blood . . . | *Piroplasma ovis* (= *Babesia ovis*, Starcovici). |
| *Petrogale penicillata* . . | Subintestinal connective tissue | *Sarcocystis mucosa* (Blanchard). |
| *Potamochoerus larvatus* . | Muscles . . | *S.* sp. [Pagenstecher, 1865]. |
| *Rhinolophus ferrum-equinum* | Intestine . . | *Coccidium viride*, Labbé. |
| *Sus domesticus* . . . | Liver and intestine | *C. perforans*, var., Rivolta. |
| ,, ,, . . . | Muscles and connective tissue | *Sarcocystis miescheriana* (Kühn). |
| *Talpa europaea* . . . | Gut . . . | *Cyclospora caryolytica*, Schaud. |
| *Vespertilio murinus* . . | Blood . . . | *Polychromophilus murinus*, Dionisi. |
| *Vesperugo* sp. . . . . | ,, . . . | *Achromaticus vesperuginus*, Dionisi. |
| *Zalophus californianus* . | Muscles . . | *Sarcocystis hueti* (Blanchard). |
| *Homo sapiens*, Man . . | Liver . . . | (?) *Coccidium cuniculi* (Riv.). |
| ,, ,, . . | Intestine . . | *C. perforans*, var. [Kjellberg 1860]. |
| ,, ,, . . | ,, . . | *C. bigeminum*, Stiles. |
| ,, ,, . . | Pleural cavities . | "*Eimeria*" *hominis*, Blanchard. |
| ,, ,, . . | Skin, etc. . . | *Coccidioides immitis*, Rixf. et Gilchr. |
| ,, ,, . . | Blood . . . | *Laverania malariae*, Gr. et Fel.; *Plasmodium malariae* (Laveran); *Plasmodium vivax* (Gr. et Fel.). |
| ,, ,, . . | Muscles . . | *Sarcocystis lindemanni* (Riv.). |
| ,, ,, . . | Liver . . . | *S. immitis* (Blanchard). |

## Literature of the Sporozoa.

The following list of references is by no means intended to be a complete bibliography of the Sporozoa, but merely to be a guide to the literature of the group, especially to the recent advances in knowledge. Hence, of the less recent works, only comprehensive treatises are cited, in which more or less exhaustive bibliographical references will be found. *Bütschli* [1] gives a complete bibliography up to 1882, and *Hagenmüller* [3] is a valuable and exhaustive summary of Sporozoan literature up to 1898 inclusive. Bibliographies more or less complete are to be found in *Delage* and *Hérouard* [2], *Labbé* [4], and *Lühe* [5], and full references to the recent literature of malarial parasites are given by *Schaudinn* [94*a*]. References to current literature will be found in the *Zoological Record* or in the *Bibliographia Zoologica* published with the *Zoologischer Anzeiger.*

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[*Monocystis légeri* n.sp. in *Carabus auratus.*]

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[The name *Légerina* is proposed for *Benedenia;* the genus is characterised by polysporous oöcysts and by lacking schizogony; it includes two species: (1) *L. octopiana* (Schn.), with from 6-12 sporozoites in the spore, occurring in *Octopus vulgaris* and *Eledone moschata;* (2) *L. eberthi* (Labbé), with 3 or 4 sporozoites, from *Sepia officinalis.* In both forms cysts are found containing macrospores with macrosporozoites and other cysts containing microspores with microsporozoites, perhaps representing a sexual differentiation thrown back to the earliest stages of the life-history.]

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[Gives a brief general account of the Sporozoa. The author appears to use the word "macrogamete" in the sense of a female merozoite; see above, p. 210, footnote.]

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[The merozoites destined to form ♀ gametocytes are distinguishable from those destined to form ♂ cells. The gametocytes are sharply distinct, and form precocious associations, but the ♂ gametocytes may form ♂ gametes apart from the ♀ cell, in which case, however, the ♂ gametes come to nothing.]

# THE PROTOZOA (*continued*)

## SECTION L.—THE INFUSORIA OR CORTICATA HETEROKARYOTA[1]

THIS group is clearly marked off from other Corticata by the occurrence of cilia, suckers, or tentacles in the active phase of life of all species. A character which is of far greater morphological importance, however, is the presence in each individual of two distinct nuclear elements called the meganucleus and micronucleus respectively.

The group is divided into two classes :—

THE CILIATA (Ehrenberg).
THE ACINETARIA (Lankester).

The Ciliata are either free or fixed forms with cilia disposed in tracts or bands on the cortex.

The Acinetaria are fixed or sedentary forms provided with suckers or tentacles. They give rise to free-swimming individuals which are ciliated.

HABITS.—The habits of the animals included in this group are very variable, and may be conveniently studied as arranged in five categories,—the free-swimming habit, the creeping or crawling habit, the stalked fixed habit, the epizoic habit, the endozoic habit.

The Heterokaryota with free-swimming habits principally belong to the group of the Ciliata. They may be found in pure pond water (*Spirostomum*, *Paramoecium* sp., etc.), swimming freely near the surface or hovering about the mud at the bottom, or even coursing about the water in the intermediate depths. A considerable number of genera are marine.

Their food consists principally of minute animal and vegetable organisms that they find floating in the water, but they will also seize and devour particles of organic matter set free by the dissolution of animal or vegetable bodies after death. Some species appear to find their maximum vitality in water containing putrefying matter, in which case their food consists chiefly of

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[1] By S. J. Hickson, F.R.S.

Bacteria. In all cases they move with a good deal of activity, sometimes with a uniform speed and sometimes with short starts and stops alternating with considerable regularity. It may be noticed that in any case one end of the animal's body is habitually in front, and that when it wants to change the direction of its progress it turns round. This enables us to speak definitely of an anterior and a posterior end as in the bilaterally symmetrical metazoa. The two ends of the body are frequently so much alike in form and as regards the disposition of the cilia (many species of Paramoecium) that in killed and preserved specimens they are almost indistinguishable. In many cases, however, the anterior end may be distinguished by being more pointed (*Spirostomum*), by the conspicuous mouth (*Prorodon*), by the presence of peculiar sensory cilia (HYPOTRICHA), or by a special collar (peristome) of long cilia on the margin of a spiral ridge (HETEROTRICHA) round the mouth. It is not always possible to define the limits of the dorsal and ventral surfaces, as the body may be almost spherical in shape, and the cilia may be of approximately equal length and evenly distributed on the surface. In such forms, the progression of the animal is accompanied by a more or less rapid rotatory movement round the long axis of the body. In other cases, however, the body is flattened (*Paramoecium*) and the dorsal and ventral surfaces fairly well defined.

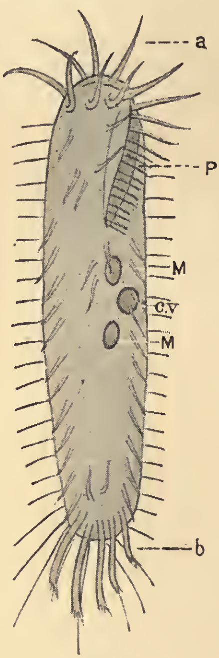

FIG. 1.

Ventral view of *Oxytricha*, a creeping Hypotrichan. *a*, frontal cirri, probably sensory in function; *b*, caudal cirri; *P*, peristome overhung by a membranella; *M*, *M*, meganuclei; *c.v.*, contractile vacuole. (After Sterki.)

Among those forms that habitually crawl or creep over surfaces, the body is generally oval in outline and considerably flattened dorso-ventrally. A further peculiarity is frequently found in the specialisation of some of the cilia to serve the purpose of locomotion, and perhaps also the functions of touch and taste (Fig. 1, *a* and *b*). These cilia are usually called cirri, and are distinguished by their thickened bases and considerable length.

Among the sedentary forms there is a decided prevalence of more radially symmetrical shapes, with a restriction of the cilia to a definite ring or series of rings round the mouth. It is in the sedentary forms, too, that we often find incomplete fission, leading to the formation of colonies of several individuals organically connected together. In some sedentary species, too, there is a secretion of a mucous substance, frequently strengthened by foreign particles, which serves as a protective tube or case. This may be autothecalous (Fig. 83), when the tube of each individual is distinct, or coenothecalous (*Ophrydium*, Fig. 2), when the secretions of the individuals composing a colony form a common test perforated by a series of tubes.

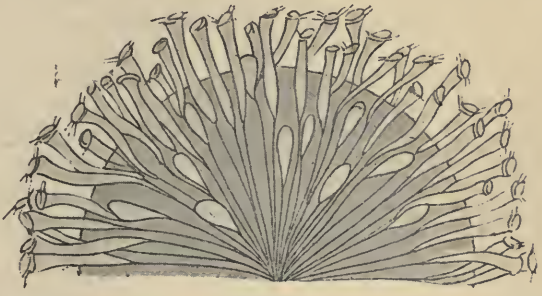

FIG. 2.

*Ophrydium eichornii*, Ehrb., a colonial Peritrichan with a coenothecalous mucilaginous test. British. Freshwater. Size of colonies about 4 mm. in length.

A large number of the sedentary forms are epizoic. Some species of *Epistylis* are found on the appendages or body wall of Cyclops and other small Crustacea, but in this instance the epizoic habit does not appear to be necessary, as the same forms may also be attached to water weeds or other objects. There are other genera, however, which are only found upon the bodies of living animals, and seem to be dependent on their host for suitable conditions of existence,—such are *Dendrocometes* and *Spirochona* on the gills of Gammarus, *Kentrochona* on the gills of Nebalia (Fig. 3), and *Cothurniopsis* on the gills of Astacus. In these cases no special modification of structure can be attributed to the epizoic habit.

A great many genera are entozoic in habit, being found only in the intestines, bladder, or blood of other animals. The remarkable consistency with which some of these forms occur in a particular situation in only one species of host, is similar to the partiality

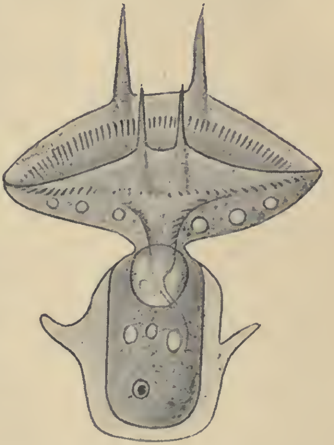

FIG. 3.

*Kentrochona nebaliae*, from the maxillipedes of Nebalia. Size about ·04 mm. (After Rompel.)

exhibited in this respect by many parasites belonging to other classes of the animal kingdom; but although the entozoic Infusoria are frequently called parasites, it is doubtful whether this term is correctly applied to them. The general conception of a parasite is an organism that gets its food and protection at the expense of its host, and that when present in considerable numbers causes injury or weakness.

There is no evidence at present that the Infusoria feed upon anything except substances that would, without their presence, be ejected from the body of the host; and it is quite possible that by disintegrating certain substances in the alimentary canal, they may be advantageous rather than deleterious to their hosts. The structure of the entozoic Infusoria is so varied that it is usually impossible to recognise in them any special adaptation to their environment. The mouthless *Opalina* found in the bladder of frogs may owe its many peculiarities of form to entozoic habits, but there is nothing of importance in the structure of *Nyctotherus*, occurring in the rectum of the same animal, that can be regarded as associated with its peculiar habitat.

Some groups of animals appear to afford much more favourable conditions for the entozoic Infusoria than others. They are rarely absent from the rectum and bladder of adult Amphibia, the intestines of white ants and other Orthoptera are frequently crowded with Trichonymphidae, and the alimentary canal of cows, horses, and other herbivorous mammalia support a large number of remarkable genera. In the coecum of the horse, Bundle has found no less than thirteen distinct species. (*Cycloposthium*, *Blepharocorys* (3 species), Fig. 4, *Paraisotricha* (3 species), *Didesmis* (2 species), *Bütschlia*, *Blepharoprosthium*, *Blepharosphaera*, and *Blepharocodon*.) They have not been found in the Carnivora. In the intestines of man, *Balantidium minutum* and *Nyctotherus faba* occasionally occur.

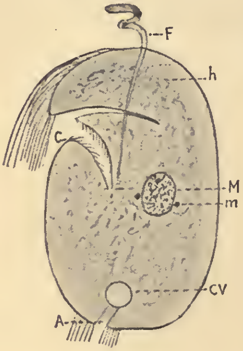

FIG. 4.

*Blepharocorys uncinata*, Fior., from the coecum of the horse. *M*, meganucleus; *m*, micronuclei; *C.V.*, contractile vacuole; *A*, anus surrounded by cilia; *C*, mouth; *h*, hood overhanging the mouth, bearing many long cilia; *F*, adhesive appendage. (After Bundle.)

SIZE.—The size varies considerably. Some of the elongated forms, such as *Spirostomum*, may attain to a length of 3 mm. when fully expanded, but the more compact oval or rounded forms rarely reach a greater size than 1·5 mm. in their longest axis (*e.g. Bursaria*). The usual size is between this and 0·04 mm. in length (*e.g. Cinotochilum*).

The substance of the body is clearly differentiated into an outer, more solid cortical sheath and an inner, semifluid medullary substance. To these the terms exoplasm and endoplasm respectively are usually applied by authors, but, as pointed out by Lankester, it is important that the permanent arrangement of the living substance in the INFUSORIA should not be confounded with the transitory arrangement of the particles forming the exoplasm and endoplasm of the GYMNOMYXA, and it is therefore advisable to retain in this connection the terms "cortex" and "medulla."

CORTEX (Ectosarc, Ectoplasm).—The cortex is, in its simplest form, a clear, firm outer layer of protoplasm, bearing the cilia or suckers, and showing no evidence of further differentiation even with the highest powers of the microscope. In some of the larger Heterokaryota, however, three distinct layers may be recognised—an outer very thin skin, called the pellicle; a lower layer, usually characterised by a series of vertical and parallel lines, called the alveolar layer; and an inner layer of clear transparent protoplasm continuous with the medulla, and distinguished from it only by the scarcity of granules and the absence of food vacuoles.

These three layers are in all cases organically continuous, and are rightly regarded as being built up of living substance.

The pellicle is rarely more than 1 $\mu$ in thickness, but most frequently it is so extremely thin as to be only just distinguishable in section. It is apparently very tough, and where it is grooved or ringed it determines the outline of the body. In some forms it gives rise to hard hook-like processes, as in the parasite *Trichodina*, or to a mailed armature, as in *Coleps* (Fig. 5).

The alveolar sheath is usually much more apparent than the pellicle, and is very frequently marked by longitudinal lines which are regarded as indications of specialised strips of contractile protoplasm. It is only in a few forms that these strips are sufficiently differentiated to be distinguished as specialised muscular fibrils. In such cases, however, they are enclosed in a canal sunk beneath the general surface of the alveolar layer, and are called myoneme threads (Fig. 6). Of great interest are the myoneme threads occurring in particular parts of the body of some genera such as the sphincter of the peristome in *Epistylis*, the "myophan" thread

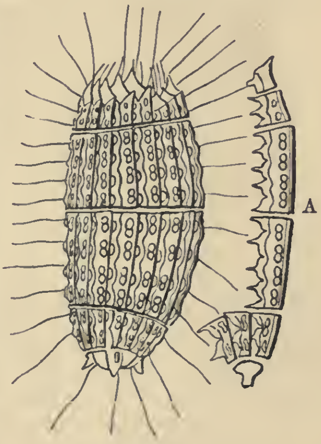

FIG. 5.

*Coleps hirtus*, Ehr., one of the mailed Holotricha. *A*, one of the 15 rows of plates. (From Bütschli, after Maupas.) × 900. Freshwater.

in the stalk of *Vorticella*, and the remarkable myoneme bands for the retraction of the peristome in *Cycloposthium*.

It is usually the alveolar sheath which bears the pigment of those forms that are specially coloured, such as the blue Stentorin of *Stentor coeruleus*, but the colour may also be due to pigments in the pellicle or in the medulla. It is in the same layer that the trichocysts occur. These are described more fully below.

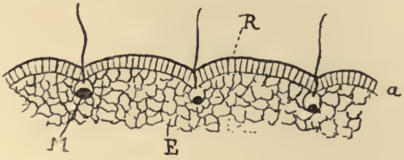

FIG. 6.

Section through the outer layers of *Holophrya discolor*. *a*, the alveolar sheath covered by a very thin pellicle; *R*, the surface ridges, between which are the rows of cilia; *M*, the vertical canals bearing the myoneme fibres; *E*, the medulla. (After Bütschli.)

The inner layer of the cortex does not present any features of very special interest. It is frequently quite inconspicuous.

The MEDULLA.—This part of the body is, in almost all cases, the larger in bulk. It is usually semifluid in consistency, and exhibits a constant rotatory movement. In *Trachelius* (Fig. 7) and some others it exhibits a reticulate character, with irregular branching pillars stretching from the centre to the cortex. In *Dendrocometes* among the Acinetaria very fine lines may sometimes be seen stretching from the arms to the region of the meganucleus, but in most cases the particles composing the medulla seem to be freely interchangeable in position.

The bodies held in suspension by the medulla are very diverse and variable. Apart from the food vacuoles, contractile vacuoles, and nuclei, which are described in some detail in another place, there are often to be found pigmented granules, colourless spherules, crystalline bodies, and smaller particles, which vary in size and number according to the state of nourishment and sexual condition of the individual.

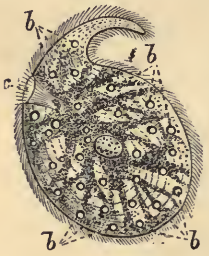

FIG. 7.

*Trachelius ovum*, Ehr., a freshwater Holotrichan, showing the reticulate arrangement of the medullary protoplasm. *b*, *b*, the contractile vacuoles; *c*, the cuticle-lined pharynx. × 80.

The *Mouth* (Cytostom) is present in nearly all the Ciliata, the parasitic *Opalina*, *Trichonympha*, and one or two other genera forming interesting exceptions to the general rule. In the Acinetaria there is usually no mouth.

In its simplest form the mouth is represented by a small slit-shaped break in the continuity of the cortex at the anterior end of the body. This can be opened for the reception of food, but in the intervals of ingestion is kept closed (*Enchelina*, etc.). In other forms the mouth, though still in its primitive position at the anterior end, is always open, and presents a clear passage from the exterior to the medulla (*Prorodon*) (Figs. 8 and 9). In *Torquatella* (Figs. 12 and 66) there is a lip-like, supra-oral lobe projecting above the mouth, and in *Trachelius* (Fig. 7), *Spirostomum*, and other genera, there is a long, pointed prostomial process. It is impossible to determine whether this prostomial process is rightly regarded as an outgrowth in front of the mouth, or whether it is due to a shifting backwards in the position of the mouth, but in such forms as *Paramoecium*, and in the Hypotricha generally, the ventral position of the mouth can only be explained on the supposition that, in accordance with the method of feeding, it has shifted its position from the primitive one at the anterior end of the body.

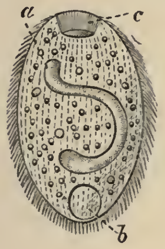

FIG. 8.

*Prorodon nivens*, Ehr., one of the Holotricha. *a*, nucleus; *b*, contractile vacuole; *c*, mouth with horny fasciculate lining. × 75.

FIG. 9.

The horny fasciculate lining of the mouth of *Prorodon* isolated.

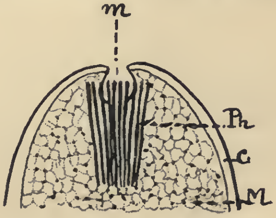

FIG. 10.

Section through the mouth and pharynx of *Urotricha lagenula*, Kent. *m*, mouth; *Ph*, pharynx; *c*, cortex; *M*, medulla. (After Schewiakoff.)

In most of the Ciliata very little differentiation can be observed in the protoplasm surrounding the oral aperture, but in a few cases a series of rod-like thickenings of the cortical protoplasm guard the mouth. In *Prorodon* (Fig. 8), for example, there is a paling arrangement of such rods which appears to serve the purpose of keeping the aperture distended. In *Urotricha* these rods make an apparatus of a more complicated type sunk below the plane of the mouth, forming what might be called a pharynx (Fig. 10). The mouth of the Infusoria may be situated either at the surface of the cortex or sunk to the bottom of a funnel-shaped depression usually called the vestibule, and on the slopes of this or in the neighbourhood of its margin many specialised differentiations of cilia or groups of cilia may be found (the paroral cilia) adapted to the function of driving the food into the mouth (*Blepharocorys*, Fig. 4).

The mouth or the vestibule is sometimes overhung by one or two membranous expansions of the cortex, the free edges of which are provided with a special row of cilia. In *Opercularia* this membrane is like a lid or operculum which closes the aperture of the vestibule before the peristome is contracted.

Another noteworthy feature of the mouth region are the tracts of trichocysts which are occasionally seen (*Dileptus*, *Amphileptus*) leading from the anterior part of the prostomial lobe to the mouth. The specialisations of cilia and other structures in the region of the mouth of these animals are so numerous, however, that a description of the conditions met with in each genus would be necessary to do justice to the subject.

There can be no doubt that in some forms, such as *Blepharocorys* (Fig. 4), *Nyctotherus* (Fig. 56), etc., a definite cytopyge or cell-anus does occur, and in others (certain species of *Entodinium*) the anus opens into a groove-like depression of the surface. As a general rule, however, there is no definite opening of this character, and the undigested parts of the food are simply pushed through the cortex at some particular region of the body.

## Cilia, Cirri, Membranes, and Tentacles.

In all the Heterokaryota there are to be found delicate protoplasmic processes from the general surface of the body, which perform the function of locomotion and ingestion of food or of sensation. These may have the form of very delicate and short whip-like threads, which are called cilia; coarse, blunt, or pointed processes, which are called cirri; expanded, flattened membranes; or the remarkable suckers and tentacles of the Acinetaria.

It is not an unreasonable hypothesis that in the ancestral forms the processes had the form of cilia, and that in the process of differentiation of the Heterokaryote body, the cilia in certain regions became fused together to form cirri and membranes, or differentiated to form suckers and tentacles. The view that the ciliated body was the most primitive is supported by the facts that the genera of the class Ciliata, which are apparently the simplest in general structure, exhibit no modification of their ciliary apparatus, and that in the highly differentiated Acinetaria the free-swimming buds are always provided with bands or tracts of unmodified cilia until they assume the sedentary habit.

The cilia in their simplest form are composed of the clearest and most homogeneous kind of protoplasm, in which no granules nor fibrils of any kind can be discovered. They spring from the pellicle, and, as Bütschli has clearly shown, are continuous with it. In many forms they undoubtedly appear to penetrate through the alveolar layer into the subjacent medulla, but this appearance can be best accounted for by the view that they are usually supported and influenced by a specialised thread of the cortical protoplasm attached to their seat of origin. They rarely exceed the extreme length of 16 $\mu$, and they vary from 0·1 $\mu$ to 0·3 $\mu$ in diameter.

Their particular arrangement on the surface of the body is one of the chief characters used in classification, and will be described under the several orders and sub-orders, but it may be mentioned here that when the cilia are arranged in definite rows or circles they are not infrequently united at their bases by a very delicate membrane or webbing which may be called a membranella.

In the remarkable parasites allied to *Trichonympha* (Fig. 11), some of the cilia appear to be of remarkable length, and unlike ordinary cilia in other respects. According to Porter, the shorter cilia of the middle region of the body are mainly responsible for the active movements so characteristic of the parasite; the longer cilia, which cover the greater part of the posterior region of the body, vibrate but little, while the cilia at the posterior extremity are absolutely motionless. The function of the motionless cilia appears to be to entangle and hold particles of food which are subsequently ingested by the cortex of the body in this region.

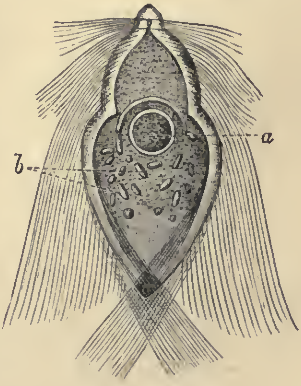

FIG. 11.

*Trichonympha agilis*, Leidy. The body is divided into three regions, an anterior translucent knob, a bell-shaped middle region with short cilia, and a posterior region with long cilia. *a*, the nucleus; *b*, granules of food. Parasitic in the intestine of white ants. × 600.

In another parasite, *Pyrsonympha vertens* (Fig. 84), the body is covered with a few short cilia, but an enormously elongated and very delicate process, called the peduncle, at the anterior end, penetrates deeply into the epithelium of the host's intestine and fixes the parasite in its position. The nature of this peduncle is difficult to determine, but it is probable that it represents an extremely specialised form of cilium adapted to the function it performs. This peduncle may be as much as 75 $\mu$ in length and 1·5 $\mu$ in diameter. A similar peduncle occurs in the Holotrichous parasite *Blepharocorys* (Fig. 4).

The cirri are very characteristic of the group Hypotricha, although occasionally found elsewhere. They usually arise from a broad base and rapidly narrow distally to an extremely fine point. In section they may be round, oval, semicircular, or even polygonal. The cirri found on the margin of *Euplotes* are regularly frayed out at the ends, and the posterior cirri of the *Oxytrichinae* are very much flattened (Fig. 1). In many of the larger forms of cirri it can be shown that a bundle of very delicate lines or fibrils runs from the base to the apex. The nature of these cirri has been a subject of some discussion among microscopists, but the view advocated by Maupas that they represent a bundle of fused cilia appears to be the most reasonable one to adopt.

The membranes which occur in some of the Ciliata in place of cilia may be regarded as due to an increase in the membranellae or webbings which are not infrequently found at the base of the rows of cilia previously mentioned (Fig. 70).

These membranes, however, are so delicate that it is difficult to find any trace of the individual cilia of which it is supposed they are mainly composed. The spiral membrane of *Spirochona* (Fig. 22) is, in form, so similar to the spirally arranged rows of cilia round the vestibule in other Ciliata, and the collar-like membrane of *Torquatella* (Fig. 12) is so like the crown of cilia in the allied genus *Strombidium* (Fig. 65), that the burden of proof that they are *not* formed by the fusion or amalgamation of rows of cilia falls upon those who maintain their independent origin.

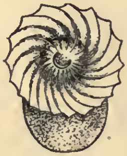

Fig. 12.

*Torquatella typica*, Lankester, found associated with the eggs of Terebella at Naples. The mouth is overhung by a crescent-shaped epistomial lobe, and there is a membranous fringe on the circumoral disc.

In the Acinetaria it appears that two phases of life regularly occur—a free-swimming phase and a fixed or sedentary phase. In the former, cilia occur arranged in bands or patches which do not differ in any essential respect from those found in Ciliata. In the latter phase, however, the cilia disappear, and a number of processes are formed which are called tentacles, suckers, or arms according to their shape, size, and general features. The morphology of these processes is not clearly understood.

In *Rhynceta cyclopum* (Fig. 13) there is only one elongated process, ending in a suctorial extremity. This process is on the one hand similar to the suckers of other Acinetaria, and on the other hand might be regarded as the attenuated hypostome bearing the mouth of this remarkable form. If we regard *Rhynceta* as a primitive form, the suckers of the Acinetaria might be regarded as formed by a multiplication of the mouths and hypostomes of a remote ancestor similar to *Rhynceta*, and the tentacles and arms as modifications of these primitive hypostomes. Such an elaborate hypothesis is not necessary, and there is no reason why all these processes of the Acinetaria should not be regarded as highly specialised cilia or cirri.

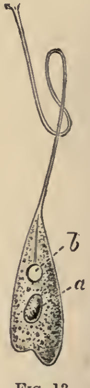

Fig. 13.

*Rhynceta cyclopum*, Zenker, an Acinetarian with a single long sucker. *a*, nucleus; *b*, contractile vacuole. × 150.

The simplest forms of tentacles are delicate pointed processes which in their fully extended condition have the same appearance as large cilia or small cirri. They differ from cilia, however, in their movements, which are intermittent and relatively slow, and also in their considerable powers of retraction, which is accompanied by the appearance of a spiral ridge (Fig. 14).

According to some authors there is a further difference from cilia in the presence in the suckers of a central lumen or canal. It is quite probable that the protoplasm in the axis of the tentacles is more fluid than at the periphery, and therefore gives the appearance of a canal; but it is very improbable that in any forms a true open lumen occurs.

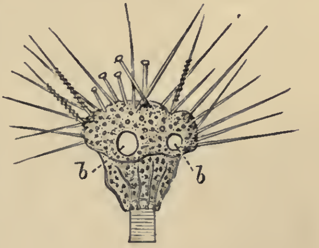

FIG. 14.

*Ephelota gemmipara*, Hertwig, a stalked Acinetarian, showing both tentacles and suckers on the disc. *b*, *b*, contractile vacuoles. (After R. Hertwig.) × 100. Marine.

The suckers differ from the tentacles in being usually uniformly cylindrical in shape, and by ending in blunt, swollen, or cup-shaped extremities. They are frequently extremely extensible (Fig. 15), and exhibit during retraction a spiral thickening similar to that of the tentacles.

The arms of *Dendrocometes* (Fig. 85) and *Stylocometes* have probably arisen by the fusion of bundles of tentacles or suckers. They bear at their extremities short papilliform or filiform processes which perhaps represent the free ends of the individual tentacles of which they are composed.

The retraction of the tentacles or suckers may be rapid or slow, and very frequently during the retraction a spirally arranged ridge appears on the surface, which may be regarded as the specially contractile filament of protoplasm which is concerned in the retraction. The arms of *Dendrocometes* and *Stylocometes* are also occasionally withdrawn to the level of the general surface of the body, but this process takes from two to three hours to accomplish, and is not accompanied by any spiral thread appearance.

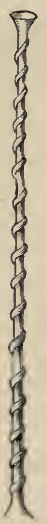

FIG. 15.

A single sucker of an Acinetarian. (After Saville Kent.) × 800.

TRICHOCYSTS occur almost exclusively in the Holotricha. They are spindle-shaped rodlets situated in the cortex close to the pellicle, having the power of suddenly shooting out a thin thread-like process when influenced by certain stimuli. In *Paramoecium* (Fig. 46) they are 4 $\mu$ in length and in *Dileptus* 12 $\mu$, but no further details of their structure have been satisfactorily described. In a few instances it has been observed that the exploded trichocysts have had a paralysing effect upon minute organisms, and by analogy it may be assumed that this is usually their function in the Holotricha; but it is quite possible that in some cases they may be used primarily or entirely as organs of defence. In *Paramoecium* (Fig. 46) they are evenly distributed in the cortex. In *Prorodon* they are confined to the anterior end, and in the Amphileptina to the ventral side of the body.

In *Epistylis umbellaria* among the PERITRICHA large oval nematocysts 85 $\mu$ in length have been described (Fig. 75). They bear a thread which before the discharge is coiled up in a capsule in the manner of the thread in the Coelenterate nematocyst. When the nematocyst has exploded, the thread is eight to ten times the length of the capsule. It is a remarkable fact that neither nematocysts nor trichocysts have been hitherto found in any other genus of the Peritricha.

NUCLEI.—In a large number of the genera included in the Heterokaryota two distinct kinds of nuclei have been observed, which differ from one another not only in size, but in form, structure, and mode of division. They are called Mega-nuclei and Micro-nuclei respectively. The micro-nuclei are frequently so small and so difficult to distinguish from other particles in the protoplasm which are stained by nuclear dyes, that their existence has been repeatedly denied in species (*Dendrocometes paradoxa*, etc.) in which they are undoubtedly present. The research of the last few years points to the conclusion that all the Ciliata and Acinetaria are Heterokaryote.

### THE MEGANUCLEUS (=MACRONUCLEUS).

The shape of the meganucleus[1] varies greatly in the order. In some genera, such as *Paramoecium* (Fig. 46), *Trichonympha*, and others, it is either oval or spherical in shape during the whole of the resting-stage. In *Carchesium*, *Vorticella*, and others it is much more elongated, and assumes the form of a curved or bent sausage. In *Stentor* (Fig. 44), *Spirostomum*, and others, it is moniliform during the resting-stage, but contracts into an oval shape before normal fission occurs. In several genera of Hypotricha and Holotricha the meganucleus divides repeatedly after, or in some cases just before, fission, and ultimately breaks up into numerous minute fragments scattered through the medulla. This condition of fragmentation persists until the animal is ready for another act of fission, when the fragments of the meganucleus fuse together again into a single spherical or oval body (Figs. 16, 17, and 18).

A similar phenomenon of fragmentation of the nucleus has been observed in the genus *Opalinopsis* (Fig. 19), but in this case unequal fission may occur without the return of the nuclear fragments to form a single compact mass.

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[1] The prefix mega- (Greek μεγας=big) is preferable to macro- (Greek μακρος=long), and is less readily mistaken for micro-.

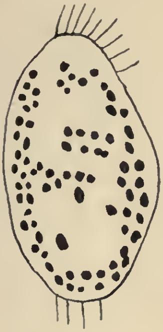

FIG. 16.

*Oxytricha scutellum*, Cohn. Prepared specimen, showing numerous fragments of the meganucleus scattered in the medulla. (After Gruber.)

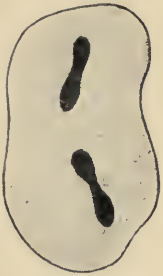

FIG. 17.

*Oxytricha scutellum*, Cohn. The fragments having fused into a single meganucleus, this has again divided into two nuclei antecedent to fission. (After Gruber.)

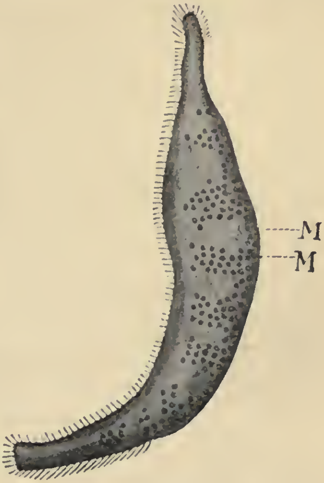

FIG. 18.

*Lacrymaria* (*Trachelocerca*) *phoenicopterus*, Cohn, from a prepared specimen, showing the meganucleus. *M*, *M*, fragmented into a large number of small granules scattered through the protoplasm. (After Gruber.)

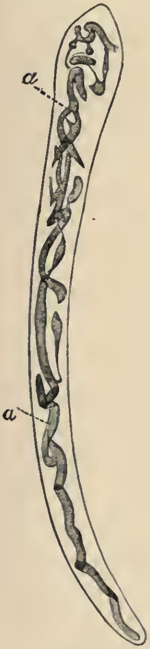

FIG. 19.

*Opalinopsis sepiolae*, Foett. × about 200, to show the remarkably branched and twisted meganucleus (*a*, *a*).

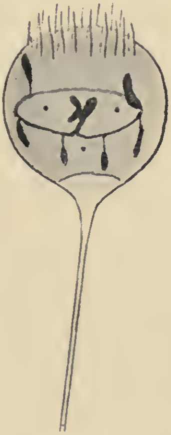

FIG. 20.

A preparation of an undescribed species of the Acinetarian genus *Ephelota*, from the Cape of Good Hope, to show the ring-shaped meganucleus, with knob-like processes, and the three minute micronuclei. (Original.) Marine. ·05 mm. across disc.

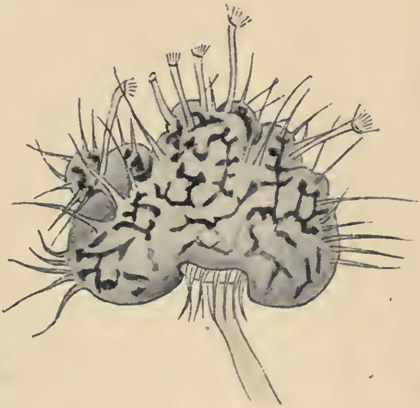

FIG. 21.

*Ephelota* (sp. ?), from a stained preparation of an individnal with 16 buds, to show the branching and anastomosing meganucleus. Size about ·5 mm. in length and ·16 mm. across the disc. (From Ishikawa.)

Among the Acinetaria many curious forms of meganucleus have been described. In full-sized specimens of a species of *Ephelota* (Fig. 20) the meganucleus has the form of a ring situated in a plane parallel with the crown of tentacles. From this ring several knob-like processes project, some turned towards the crown and others towards the stalk.

In another species described by Ishikawa the meganucleus of the adult is in the form of a coarse-beaded network (Fig. 21). In *Dendrosoma* it is a thick smooth band occupying the axis of the branches.

In some cases remarkable changes in the shape of the meganucleus occur which seem to have no connection with the reproductive processes. In *Dendrocometes*, for example, it may take the shape of an elongated spindle and move to almost any position in the cytoplasm. It has even been seen to retreat entirely into one of the arms. It may also be assumed, from its very irregular form in many species of *Acineta*, *Ephelota*, and other genera, that the meganucleus normally undergoes amoeboid contortions during the whole period which elapses between successive acts of reproduction.

Very different accounts have been given of the minute structure of the meganucleus in the group. It is clear, however, that at least two elements enter into its composition—a substance that may be called the Chromatin, having a great affinity for ordinary nuclear stains; and a substance which resists nuclear stains, and may be called the Achromatin. The chromatin is usually in the form of a close-meshed network of fibrils extending through the whole space occupied by the meganucleus, and it gives with low powers of the microscope the appearance of a crowd of granules. Under unfavourable circumstances this network may be gathered up into a series of bunches, and each bunch may be ultimately torn away from its neighbours, giving the chromatin the appearance of being arranged in a series of irregular and frequently vacuolated granules. If the unfavourable circumstances continue, disintegration of the meganucleus may follow, but recovery from the granular condition is quite possible, and the chromatin may again resume the form of an evenly distributed network. Changes in the shape of the meganucleus may lead to the deceptive appearance of change in structure. Thus the meganucleus of *Dendrocometes* when it assumes the spindle form appears longitudinally striated, and in its constriction during bud-formation there is an appearance that might be mistaken for a row of independent fibres in the narrowest part of the neck (Fig. 31). Careful analysis of these striae and rod appearances proves, however, that in all cases they are due to a rearrangement of the meshes of the primary network. Local thickenings of the fibrils of the chromatin network frequently occur, and in some forms acquire considerable size, but it seems probable that chromatin granules entirely disconnected from the network only occur in a few forms.

In *Spirochona* there is a remarkable arrangement of the elements of the meganucleus, the chromatin being collected into a thin, saucer-shaped mass, leaving a spherical space of clear achromatin in which during the resting-stage a large deeply-staining spherule occurs (Fig. 22). The nature of this granule is very uncertain. By Balbiani it was regarded as combining the characters of the centrosome and nucleolus of the Metazoan cell. Before the division of the meganucleus (Fig. 23) it disappears, and cannot be traced again until after the separation of the daughter meganuclei. In this respect it undoubtedly claims to be ranked in the category of nucleolar structures; but its claim to rank as a centrosome as well is, for many reasons, unsatisfactory.

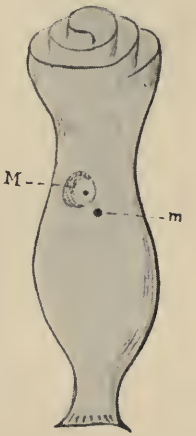

Fig. 22.

*Spirochona gemmipara*, Stein, from a stained preparation, to show the meganucleus (*M*) in a state of rest and one micronucleus (*m*). Size about 0·05 mm. in length. (Original.)

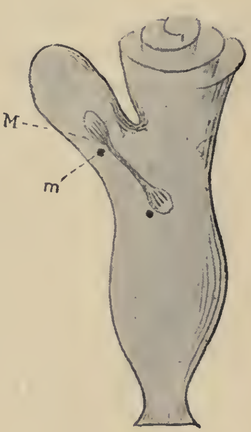

Fig. 23.

*Spirochona gemmipara* during the formation of a gemmula, showing that, during the division of the meganucleus, the nucleolar body is absent. (From an original preparation.)

It is still an open question whether any of the meganuclei are surrounded by a definite membrane of a distinct texture. The appearance of a membrana limitans, which may be seen in all stained specimens mounted whole, is not always seen when the meganuclei are cut into thin sections, and it may therefore be accounted for as an optical effect due to the difference in density between the nucleoplasm and the surrounding cytoplasm. This explanation, however, will not account for the facts observed in all cases, and it seems to be certain that a membrane of a distinct chemical character is formed between the nucleoplasm and cytoplasm in some species. It is, however, always extremely thin and flexible.

THE MICRONUCLEUS.—Whilst it cannot yet be said that a micronucleus has been proved to exist in all Ciliata and Acinetaria, the careful researches of recent years renders it extremely probable that one or more micronuclei form an essential feature of their organisation. The difficulty of determining this important fact with certainty is that, during the long period of rest which the micronuclei pass through between the acts of fission, gemmation, or conjugation, the chromatin, as well as the achromatin, elements shrink into such a small compass that they are not easily seen. The usual appearance of a micronucleus in the resting-stage is that of a minute irregular granule lying in the centre of a perfectly clear vacuole. No lines nor dots can be seen in the vacuole, but it seems probable from events which occur during division that the clear substance contained in the vacuole is the same as the achromatin of the karyokinetic figure.

The size of the micronucleus in the resting-stage is rarely more than 10 $\mu$, but more frequently it is 1 $\mu$ or even less in diameter. It is 2 $\mu$ in *Dendrocometes*, 4-5 $\mu$ in *Prorodon*, and 12-14 $\mu$ in *Paramoecium bursaria*, in which species it seems to reach its maximum size.

The staining reactions of the micronucleus in rest are the same as those of the chromatin of the meganucleus.

The number of micronuclei in the individual varies considerably. In most species there is only one (*Paramoecium caudatum*, *Colpidium colpoda*, *Vorticella monilata*, etc.); in others there are normally two (*Paramoecium aurelia*), or three (*Spirochona*), or any number up to as many as twenty-eight (*Stentor roeselii*). The number is not always constant in the same species. Maupas, for example, found three micronuclei in some individuals of *Paramoecium aurelia*. In *Dendrocometes* the number varies from two to five; *Spirochona gemmipara* has, according to Hertwig, normally three micronuclei; but in several specimens examined in Manchester, Hickson could only find one.

DIVISION OF THE NUCLEI.—There is a very important difference to be observed in the division of the meganuclei and micronuclei. The meganuclei divide only during fission or gemmation, except in those cases mentioned above in which the meganucleus breaks up into a few or many pieces, after fission of the individuals. In all cases the division is strictly amitotic. In some cases a concentration of the chromatin occurs along lines parallel with the longer axis of the meganucleus, giving the appearance of longitudinal striations or thin delicate chromosomes with anything but the higher magnifying powers. In some cases (*Spirochona*) these lines are crowded together at the narrowest part of the constriction, and may have the appearance of a broad equatorial plate. In *Spirochona*

(Fig. 23) and *Kentrochona* we also find a clear globule of achromatin substance at the poles, but there are no true linin fibrils. In most cases the meganucleus in fission or gemmation divides by simple constriction into two approximately equal parts, but in *Opalinopsis* (Fig. 19) and *Anoplophrya* (Fig. 30) it divides into a number of unequal parts, and in *Ephelota* (Fig. 20), *Podophrya*, and others a number of pieces are constricted off from it, each of which gives rise to the meganucleus of a bud.

The division of the micronucleus is always mitotic. The first changes that are noticed are increase of size and the resolution of the chromatic granule into a network of anastomosing fibrils. The increase in size is usually considerable. In *Colpidium*, for example, the diameter increases three- or four-fold (Hoyer). In *Dendrocometes* the micronucleus increases from 2 μ to 10 μ in diameter.

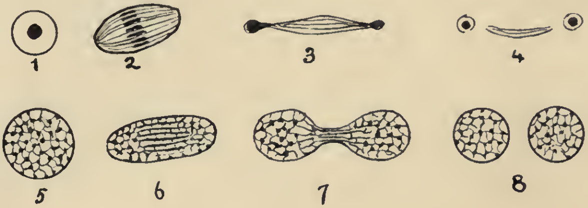

Fig. 24.

Diagram to illustrate the structure and division of the nuclei of the Infusoria. 1, a micronucleus in a state of rest, consisting of a spherule of chromatin in a clear vacuole; 2, formation of the spindle of linin fibrils, with a band of chromosomes on the equator; 3, the chromatin separated into two compact masses at the poles of the spindle; 4, formation of the vacuole round the chromatin, and dissipation of the spindle; 5, a spherical meganucleus in a state of rest; 6, elongation of the meganucleus previous to division; 7, constriction of the meganucleus; 8, division into two daughter meganuclei.

After the increase of the micronucleus in size is completed, a clearly-defined spindle of linin fibrils appears and the chromatin network breaks up into a number of small chromosomes arranged in an equatorial plane (Fig. 24). The chromosomes are so small and their number is so great that they can neither be accurately counted nor their method of fission determined. It seems probable, however, that the two parties which travel towards the poles are exactly equal in number. No satisfactory accounts have yet been given, in the division of the micronucleus, of structures corresponding with the centrosomes of the karyokinetic figures of other cells, and in many cases that have been very carefully investigated centrosomes are certainly absent. It is one of the most striking features, perhaps, of the nuclear phenomena of the Heterokaryota that centrosomes do not occur. The two parties of chromosomes travel with considerable rapidity to the poles of the spindles, and there, in many cases, they become compressed into a tiny compact mass, leaving the spindle between them free from chromatin. The spindle is, in this condition, frequently very much elongated, stretching more than half-way across the medulla. In *Dendrocometes* it is at this stage as much as 30 μ in length (Fig. 31). The spindle disappears suddenly and seems to be completely absorbed by the cytoplasm immediately, or very soon after, it is disconnected from the chromatin granules at the poles.

### THE NUCLEI OF OPALINA.

If the current views concerning the nuclei of *Opalina* are trustworthy, this genus should no longer be regarded as a member of the Heterokaryota. *Opalina* possesses, according to Pfitzner and others, a large number of meganuclei, but no micronuclei. Moreover, the meganuclei divide by a typical process of mitosis. These views may possibly be erroneous. Thin sections of Opalina that are suitably stained show, in addition to the numerous meganuclei, a large number of small bodies containing chromatin. These are probably micronuclei (Fig. 25). The meganuclei divide sometimes amitotically, and it is probable that they always do so. The mitotic figures discovered by Pfitzner are clearly seen in a large number of sections examined, but they are smaller than the meganuclei and are probably formed by micronuclei which, as in other forms, increase considerably in size before division. The matter requires, however, further investigation.

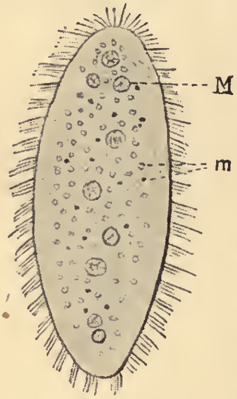

FIG. 25.

Vertical section through *Opalina ranarum*, ×100, to show the large meganuclei (*M*) and the numerous minute chromatin bodies (*m*), which are probably the micronuclei. (Original.)

CONTRACTILE VACUOLES.—The contractile vacuoles occur in all Heterokaryota except in *Opalina*, *Opalinopsis*, some of the marine Hypotricha, and a few others. They are simply spaces formed at some localised spot or spots in the medulla by the accumulation of a fluid, and they discharge their contents to the exterior when they have reached a definite limit of size. The fluid that accumulates in these spaces is probably charged with waste products of the metabolism of protoplasm. Although the positions in which these vacuoles appear are fairly constant for each individual, they have no proper walls, and must not be regarded as definitely formed organs. The number varies enormously in the group (1–100 or more), and when there are more than three or four in any one species the number may vary in the individual (Fig. 26). In some of the large species the number of the contractile vacuoles increases with the size and age of the individual, but in *Nassula*, *Dendro-*

*cometes*, and others which reach a considerable size there is never more than one.

In the majority of cases the contractile vacuole is spherical in shape and situated in the medulla. It slowly expands (diastole) until its periphery comes in contact with the pellicle at the surface, when it instantaneously collapses (systole). In some forms (*Spirostomum*, etc.) a long canal may be seen, towards the close of diastole, to be connected with the spherical vacuole. This appears to be formed by the fusion of a row of small secondary vacuoles stretching from the anterior to the posterior end of the body. In *Stentor* the contractile vacuole has a very elongated, rod-shaped form (Fig. 44).

In the VORTICELLIDAE it is situated in the neighbourhood of the vestibule, but instead of opening directly into it when systole occurs, it opens into a reservoir which is in communication with the vestibule. In *Blepharocorys* (Fig. 4) and some other forms the contractile vacuole opens into the passage which leads to the anus. In *Paramoecium* (Fig. 46, 3) and a great many other forms a series of six or more canals or spindle-shaped secondary vacuoles appear in a radiating form round the principal contractile vacuole, and may be seen to discharge their contents into the primary vacuole immediately before its collapse.

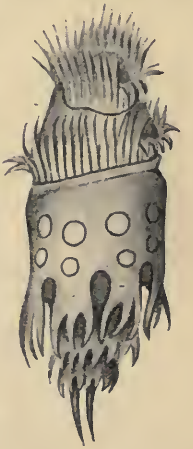

FIG. 26.

*Ophryoscolex purkinjei*, Stein, from the rumen of an Artiodactyl, an oligotrichous Infusorian with several contractile vacuoles. (After Bütschli.)

There can be little doubt that the function of the contractile vacuole is primarily the excretion of waste products, but by assisting the osmosis of fresh water through the protoplasm it may be regarded as being also respiratory in function. As shown by A. G. Bourne, when anilin blue is added to the water in which the animal lives, the contents of the contractile vacuoles are deeply stained.

The systole of the contractile vacuole is not caused by any active contraction on the part of the protoplasm of the medulla, but, according to Bütschli, it is due to the physical attraction of the small droplet of fluid to the mass of water at the periphery. It is of the same general nature as the phenomenon of capillarity. The action cannot take place until the vacuole has, by its diastole, reached the periphery, and the drop of fluid is thereby brought into contact with the surrounding medium.

The rapidity of the successive contractions of the contractile vacuoles is variable. According to Rossbach it always increases with a rise in temperature. In *Euplotes charon* the intervals between each contraction were 61 seconds at 5° C., and regularly diminished to 23 seconds at 30° C. In *Stylonychia* they diminished from 18 at 5° C. to 4 at 30° C.

Digestion.—The food of the Ciliata usually consists of minute organisms such as Bacteria, other Infusoria, etc., or particles of organic substance which are able to pass through the mouth into the medulla. As they enter the medullary protoplasm they are accompanied by a globule of water and give rise to the so-called food vacuoles. The food vacuoles pass along a definite course and ultimately reach the anus, or some position in the cortex where a temporary anal aperture can be formed. If a *Carchesium* (Fig. 27) be fed with finely-powdered food material that is stained, the following changes can be observed. Shortly after ingestion the particles are aggregated into a lump at the centre of the vacuole by the centripetal flow of a liquid from the surrounding cytoplasm. A secretion of an acid into the vacuole then occurs and the food particles undergo partial solution (Fig. 28). In the next stage absorption of the dissolved food into the protoplasm takes place, and then the vacuole, with the undigested remnants, travels to the region of the vestibule, where a temporary anus is formed for the discharge of its contents.

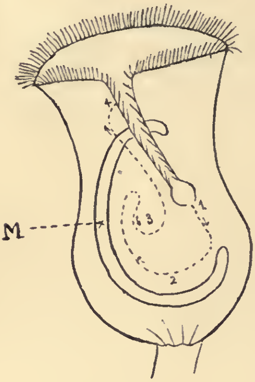

Fig. 27.

Diagram of *Carchesium* to show the course taken by the food vacuoles. 1, the region of ingestion; 2, of aggregation; 3, of solution; 4, ejection. *M*, the meganucleus. (After Greenwood.)

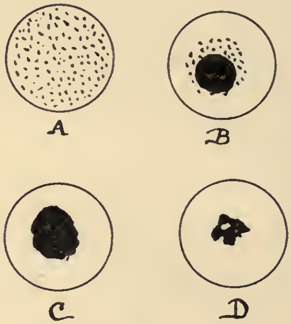

Fig. 28.

Four stages in the food vacuole of a *Carchesium* fed with white of egg and Indian ink. *A*, immediately after ingestion; *B*, first phase of aggregation; *C*, second phase of aggregation; *D*, just before ejection. (After Greenwood.)

In the mouthless *Opalina* the food is probably absorbed in a liquid form from the surrounding medium. In some of the Trichonymphidae solid food is entangled by the motionless cilia at the posterior end of the body and then enveloped by the protoplasm in an amoeboid fashion.

Reproduction.—In the simplest forms of Infusoria the mode of reproduction in the motile phases of life is simple transverse fission, but in the higher forms other methods of division occur which are usually called longitudinal fission, simple gemmation, multiple gemmation, and spore-formation respectively. All of these, however, are probably modifications of the same essential process, which consists in the division of the three elements of the body—cytoplasm, meganucleus, and micronucleus—into two or more than two parts.

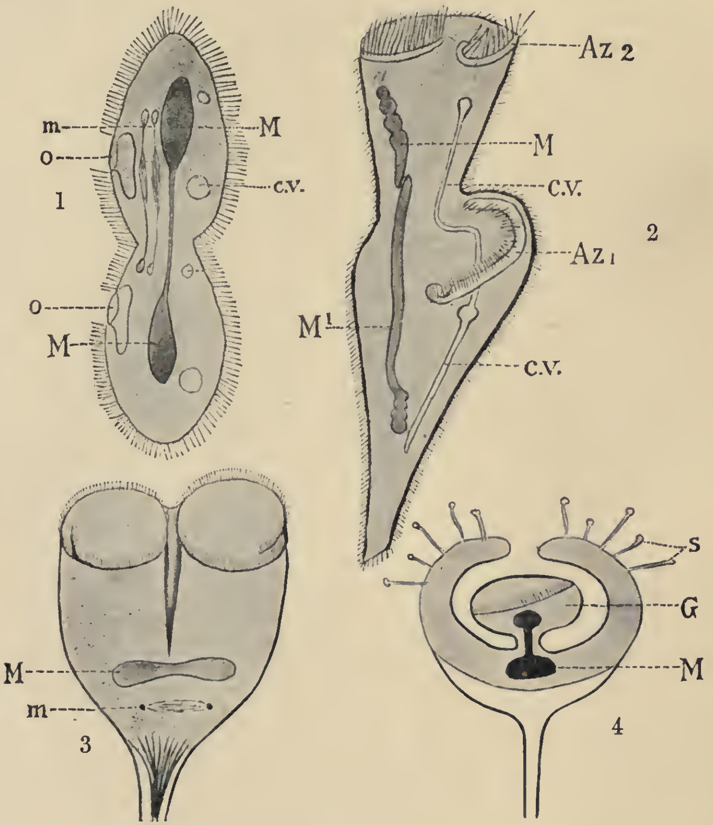

Fig. 29.

Diagrams to illustrate the principal modes of division in the Heterokaryota. 1, equal transverse fission as in *Paramoecium;* 2, unequal fission as in *Stentor;* 3, longitudinal fission as in *Vorticella;* 4, endogenous, unequal, and heteromorphic fission as in *Tokophrya.* *M*, meganucleus; *m*, micronucleus; *o*, mouth; *c.v.*, contractile vacuole; *G*, gemmula; *Az*, adoral zone. (After Lang.)

In *Paramoecium* and *Stylonychia*, which may be taken as examples of HOLOTRICHA and HYPOTRICHA respectively, fission is preceded by the formation of a second mouth (Fig. 29, 1), and the growth of a new set of cilia or cirri round and in the neighbourhood of this second mouth, similar in size and arrangement to those in the neighbourhood of the original mouth; and by the division of the contractile vacuole. In the next phase the micronucleus or micronuclei enlarge, then elongate and show the characteristic features of their mitotic division. Next, the meganucleus elongates and becomes constricted in the middle. While these changes in the nuclei are taking place, a constriction of the cortex appears at a point which is approximately half-way down the longitudinal axis of the body. The micronuclei, the meganucleus, and finally the protoplasm of the body, then divide in succession, and the two individuals that are formed separate and swim away. In the process thus described the cortical protoplasm apparently leads the way by the formation of new cilia and a new mouth. On the other hand, the micronuclei have usually formed the mitotic figure before actual constriction of the body is apparent. If the minute structure of the meganucleus be examined in the earlier stages of fission, it may be noticed that it also is not indifferent to the changes going on elsewhere. It is therefore impossible to state with certainty that either the nucleoplasm or the cytoplasm of the organism initiates the process; in fact, it seems probable in the present state of our knowledge that the impulse to divide affects all parts simultaneously.

In *Spirostomum* and *Condylostoma* the very much elongated moniliform meganucleus is contracted into a short rod-like form before fission occurs. In *Stentor*, too, fission is preceded by a contraction of the long moniliform meganucleus (Figs. 44 and 29, 2) into a thick spherical lump; but the meganucleus again elongates and divides transversely into two moniliform bands before the act of fission actually takes place. In *Oxytricha* (Figs. 16, 17, 18) and some other HYPOTRICHA the meganucleus during the active phases of life is scattered in the form of small granules through the medulla. Before fission takes place these granules collect together and fuse to form a single lump. This consolidated nucleus then divides once or twice, and fission of the whole body follows.

Fission is not, however, always preceded by the fusion of scattered meganuclei or the contraction of elongated ones. In *Opalina* the scattered meganuclei appear to be indifferent to the division of the body, and in *Opalinopsis* (Fig. 19) and *Anoplophrya* (Fig. 30) the meganucleus divides into fragments, one or more of which become the meganuclei of the daughter individuals.

In *Paramoecium* and most of the HOLOTRICHA the transverse fission results in the production of two equal individuals, but in the transverse fission of Stentor and other Heterotricha the anterior or oral extremity is decidedly smaller than the other. In *Hoplitophrya* the division is also unequal, but the smaller individual is at the end usually regarded as the posterior end. In *Anoplophrya nodulata* there is multiple transverse fission (Fig. 20), the result being one large individual and four or five smaller ones. Similarly in *Opalinopsis* the posterior end of the body gives rise to a series of small individuals which constrict off from the parent.

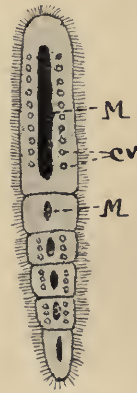

FIG. 30.

*Anoplophrya nodulata*, O. F. Müller, from the intestine of Oligochaeta, exhibiting unequal fission of the body and division of the elongated meganucleus (*M*, *M*) without previous concentration. There are numerous contractile vacuoles. (After Clap. and Lachmann.) ×ca 150.

The mode of reproduction in *Spirochona* is very remarkable. A large lump grows from the body wall just behind the spiral membrane (Fig. 23), and this increases until it reaches a size almost as large as the parent form. Judging from external appearance alone, it might be considered that this is a process of gemmation essentially different from the transverse fission of the HOLOTRICHA, but the meganucleus and the micronuclei divide equally during the growth of the so-called bud, and no difference can be observed in size or quality between the nuclear portions that are distributed to the two resultant individuals. The process cannot therefore be separated from fission, notwithstanding the fact that the manner of growth of the parent antecedent to reproduction is very exceptional. In the VORTICELLINA the manner of reproduction is usually designated longitudinal fission. The external phenomena begin with the division of the spiral zone into two equal spirals, and proceed through the disc to the stalk, and may (in some of the solitary forms) continue to the base of attachment, or (in the colonial forms) be arrested before the attached end of the stalk is reached. In the majority of the solitary *Vorticellina* the stalk does not divide. The left daughter individual develops an aboral ring of cilia and swims away, whilst the right daughter individual remains with the parent stalk intact.

There is not any morphological distinction between the longitudinal fission of the PERITRICHA and the transverse fission of the HOLOTRICHA. It is very probable that, if there is any justification at all for the comparison of the body axes of such simple forms of life, the longitudinal axis of PERITRICHA is homologous with the dorso-ventral axis of the HOLOTRICHA, and the fission is from a morphological point of view a transverse fission.

The examples of unequal transverse fission which have been quoted as occurring in HETEROTRICHA lead to the consideration of an interesting modification of the process which occurs in the

Acinetaria. The simple fission into two approximately equal halves occurs in a few simple forms only in this class (*Sphaerophrya*, etc.); in others (some forms of *Acineta*, *Tokophrya* (Fig. 29, 4), etc.) the smaller of the two segments is enclosed in a pouch-like cavity of the larger segment.

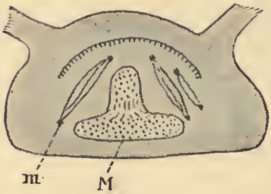

Fig. 31.

Vertical section through *Dendrocometes paradoxus*, Stein, in an early stage of reproduction. The transversely striated curved line represents the first indication of the band of cilia of the future gemmula. The meganucleus (*M*) has begun to constrict; the three micronuclei (*m*) are in the final phase of their mitosis.

In *Dendrocometes* (Fig. 31) the difference in size between the two segments is even more pronounced. The three micronuclei undergo their phases of mitosis preparatory to division, in a plane at right angles to the gill of the host to which the animal is attached. The meganucleus becomes elongated and then sends out a broad pseudopodial process in the same direction. While these nuclear changes are taking place, a curved, transversely-striated band appears in the protoplasm, which is continued after division of the nuclei into a complete circle embracing three micronuclei and one meganucleus. The protoplasm enclosed by this band is then detached from its surroundings and rotates slowly for a time by means of an equatorial girdle of cilia. It then breaks through the body wall of the parent and swims away. This remarkable ciliated daughter segment may be called a "gemmula" (Fig. 36).

In *Dendrosoma* (Fig. 32) several daughter segments enclosed in incubatory pouches are formed in different parts of the branching body at the same time, and these cannot be regarded as essentially distinct in their nature or in their mode of formation from the single internal daughter segment of *Dendrocometes*. The reproduc-

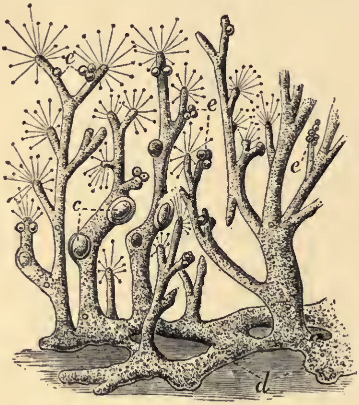

Fig. 32.

*Dendrosoma radians*, Ehrb. Size varies from 1-2 mm. in height. *d*, base of attachment; *c*, ciliated gemmulae in their pouches; *e*, smaller bud-like bodies of doubtful significance. (After Saville Kent.)

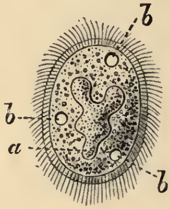

Fig. 33.

Free-swimming ciliated gemmula of *Dendrosoma*. *a*, meganucleus; *b*, *b*, *b*, contractile vacuoles. (After Saville Kent.) × 600.

tion of *Dendrosoma* therefore appears to be a process of multiple, internal, unequal fission. In several species of *Ephelota* and others, not one but several small daughter segments are formed simultaneously (Figs. 34 and 21) at the free extremity of the body, and these are liberated when they have reached a certain size.

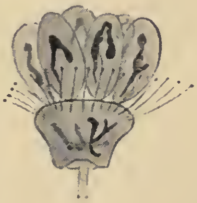

FIG. 34.

*Ephelota* (sp.?), bearing six gemmulae almost ready for liberation. (From an original drawing and preparation by Dr. Ashworth.)

In the literature of ACINETARIA the smaller daughter segments receive the names "buds," "gemmulae," or "embryos," and the processes by which they are formed are called internal or external, multiple or simple, gemmation. Whilst recognising the utility of retaining such a name as gemmulae for them, it must not be forgotten that the process of gemmation in the Heterokaryota is essentially the same as that of fission.

ENCYSTMENT AND SPORE-FORMATION.—There can be no doubt that a very large number of the Infusoria have the power of encystment. The encystment may be accompanied by reproduction, a large number of small individuals being formed during the period and escaping from the cyst wall at the end of it, or it may be simply a resting-stage from which only one individual escapes. In many CILIATA (*Colpoda*, *Prorodon*, etc.) both kinds of cysts may occur in the same species, and it is difficult to draw any definite line between them, but in the majority of species it seems probable that the cysts are either purely resting cysts or reproductive cysts.

Encystment may be caused by the concentration of the salts in water previous to drought, as proved experimentally by Cienkowsky; by the diminution in the food supply, as proved by Maupas for the OXYTRICHINAE; or, in the entozoic forms, by the change from their natural habitat into fresh-water. Encystment is never, in any Ciliata, a necessary sequence of conjugation. In the process of encystment the cilia are withdrawn and the protoplasm of the body contracted into a spherical or elliptical shape, while one or more walls are secreted by the pellicle. The outer wall or ectocyst may be soft and gelatinous as in certain Vorticellina, or it may be hard, facetted, or thorned (Fig. 73). The inner walls or endocysts are usually thin and membranous.

The resting cysts are capable of resisting the effects of dry air for a considerable length of time. Nussbaum, for instance, found that the cysts of *Gastrostyla vorax* were alive at the end of two years, and Maupas successfully hatched out *Gastrostyla steinii* from cysts that had remained dry in a watch-glass for twenty-two months. Nussbaum, however, found that in twelve years all the encysted *Gastrostyla vorax* were dead.

The method by which reproduction takes place in the reproductive cysts is not known with certainty, but it is probable that there is a rapid succession of simple fissions of the protoplasmic contents of the cyst, leading to the production of numerous swarm-spores, as is stated to be the case in *Holophrya multifiliis* (Fig. 36).

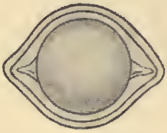

FIG. 35.

Cyst of *Dileptus anser*, O.F.M., provided with an outer shell or ectocyst and an inner membrane (endocyst) attached to the ectocyst at the poles. (After Cienkowsky.)

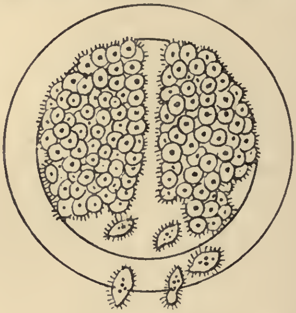

FIG. 36.

Cyst of *Holophrya multifiliis*, Fouq., as found at the bottom of aquaria in which fish affected with *Holophrya* are living. From the cyst numerous ciliated swarm-spores are escaping. (After Fouquet.) × about 75.

CONJUGATION.—A single individual Ciliate Infusorian can produce a large number of generations of daughter individuals by the process of fission, but there is reason to believe that the number is limited, and that after a time the power of fission slackens and ultimately ceases. Under normal conditions, however, the individuals exhibit a tendency to conjugate after several generations have been produced by fission, and if we are justified in regarding the individuality of two conjugating INFUSORIA as the same after conjugation as before, it may be said that the result of conjugation is a renewal and a stimulation of the powers of fission of the conjugating individuals. Although our knowledge is still far from complete, it seems certain that a process of conjugation occurs in all HETEROKARYOTA, and that this process is essential for the continuance of the vitality of the species.

There can be no doubt that the impulse to conjugation is in a large number of cases periodic, the individuals of a swarm showing for several days together no tendency to conjugation, and then simultaneously collecting together in pairs and conjugating. The cause of the impulse is obscure. Maupas expressed the opinion that a diminution in the food-supply is the primary cause of the impulse, and that individuals can be prevented from conjugating by increasing the supply of food when the tendency first makes its appearance.

According to the researches of Maupas the epidemic of conjugation in *Stylonychia pustulata* reaches its height after 175 fissions. This author also states that conjugation can be prevented by a suitable increase in the food supply, and that senile decay and death occur after 316 fissions.

On the other hand, Joukowsky has recently failed to induce conjugation by hunger in *Pleurotricha* after experimenting for eight months and reaching the 458th generation, and Calkins has cultivated *Paramoecium caudatum* to the 620th generation, without conjugation, by changing the food when the periods of depression set in.

There is some reason to believe that the onset of the epidemic of conjugation in certain CILIATA is associated with a material diminution in size; the largest specimens of a species having the power or vital force to divide by fission, do not need the stimulus of conjugation for further reproduction.

In the long series of varieties that the process of conjugation presents in the HETEROKARYOTA, attention may be called to three conditions which, when separated from the series, appear to present essential differences. In most of the free-swimming CILIATA all the individuals of a swarm in which there is an epidemic of conjugation are of the same size and structure, and it is probable that any one individual can conjugate with any other. There is no distinction of sex whatever.

In the conjugation of *Spirochona* two individuals apparently identical, situated close to one another on the same gill of Gammarus, bend towards each other and conjugate by their oral discs. Subsequently one of the two individuals separates from the gill and becomes absorbed (partially or wholly) by the other one, and from that moment it ceases to exist as an individual. In this case no external features of sexual differentiation have been observed, and perhaps do not exist, between individuals that are capable of conjugating with one another; but after conjugation has begun the important difference between the one that absorbs, which has been compared to an ovum of the metazoa, and the one that is absorbed, which has been compared to a spermatozoon, is exhibited (cf. p. 393).

In the third case, as exhibited by *Vorticella* and some other PERITRICHA, the difference between individuals that can conjugate is well marked long before conjugation actually occurs (Figs. 43 and 76). The stalked form, which may be called the female individual, is not capable of conjugating with another individual of the same kind,[1] nor, on the other hand, are the small free-swimming forms that are periodically produced—the males—capable of conjugating with one another. The only way in which conjugation can be effected is by one female individual conjugating with one male individual. In other words, the differentiation of sex appears to be complete in the case of *Vorticella* and some other forms.

During the process of conjugation very important and complicated changes occur in the nuclei of both individuals, and in all probability

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[1] It is possible that in some species a conjugation of the females may occur (see Plate lxxiii. Fig. 96 of Bütschli's "Infusoria").

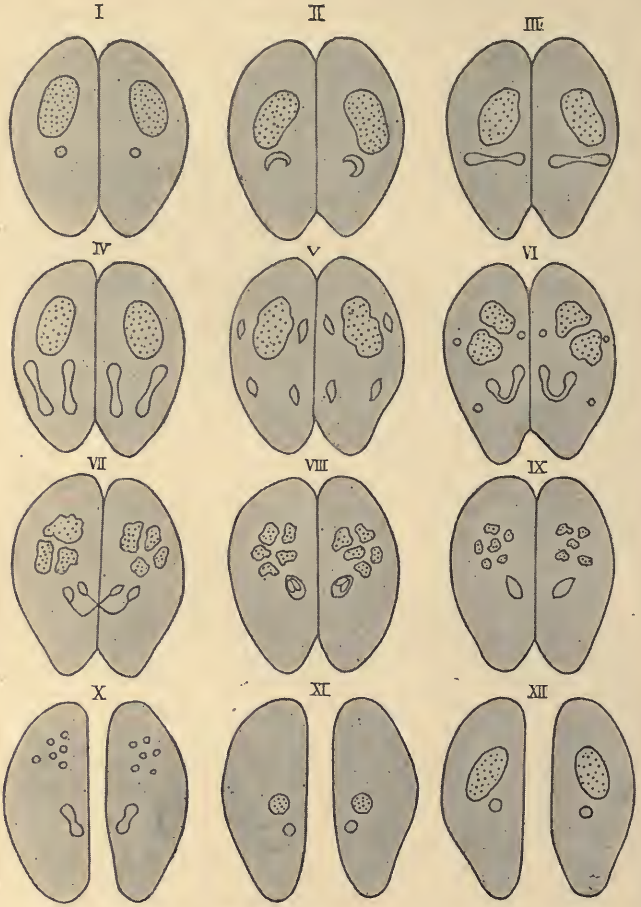


FIG. 37.

Diagram to illustrate the nuclear phenomena of the *Ciliata*, from the "Traité de Zoologie Concrète," based on the researches of Maupas. I, two individuals at the commencement of conjugation, showing a single large meganucleus and a single small micronucleus. II, stage in which the micronuclei have begun their mitosis. III, stage at the close of the first mitosis of the micronuclei. IV, stage at the close of the second mitosis of the micronuclei. V, stage in which there are four nuclei formed by the division of the micronucleus, and the meganucleus is becoming irregular in outline. VI, stage in which three nuclei are undergoing degenerative changes, and one—the sexual nucleus—is again dividing. VII, stage in which the sexual nucleus has divided into a migratory and a stationary nucleus, and the migratory nucleus of each individual has crossed into the cytoplasm of the other. VIII, stage in which the stationary and migratory nuclei have come in contact with each other. IX, stage in which the cleavage nucleus has been formed by the fusion of the migratory and stationary nuclei. The meganuclei have now broken up into a number of small fragments. X, stage in which the individuals have separated and the cleavage nucleus is undergoing its first mitosis. XI, the fragments of the old meganuclei have entirely disappeared, and a new meganucleus and a new micronucleus are forming from the daughter nuclei of the cleavage nucleus. XII, final stage with a full-sized meganucleus and a micronucleus.

in the cytoplasm as well. For the elucidation of these changes it is convenient to consider, in the first place, the phenomena that have been observed in certain Holotricha (cf. Fig. 37). When two individuals have effectively conjugated, the micronucleus of each swells up and undergoes division by mitosis into two micronuclei (II., III.). This is immediately followed by a division into four (IV., V.). Of these four nuclei three degenerate and are either absorbed or rejected from the body (VI., and Fig. 38). The remaining one—which may be called the sexual nucleus—undergoes another division into two nuclei. One of these crosses the line of junction of the conjugating individuals and enters the cytoplasm of the other individual, and may be called the migratory nucleus. The other remains in the cytoplasm of the parent, and may be called the stationary nucleus. Thus, as a result of the divisions of the original micronucleus of each of the conjugating individuals, five nuclei are formed: three degenerate and disappear, one migrates, and the remaining one is stationary. A fusion of the migratory nucleus of one individual and the stationary nucleus of the other then takes place to form the cleavage nucleus (VIII., IX.), and soon after this has occurred the two individuals separate. The cleavage nucleus soon divides into two (X.), and generally a second time into four, or a third time into eight. Ultimately, however, one of the halves of a division gives rise to the new meganucleus, and the other to the micronucleus of a daughter individual. The new meganucleus can therefore be traced back to its origin from micronuclear elements, and to this there is no exception. The meganucleus of a conjugating individual never gives rise to the meganucleus of an individual that has been released from conjugation.

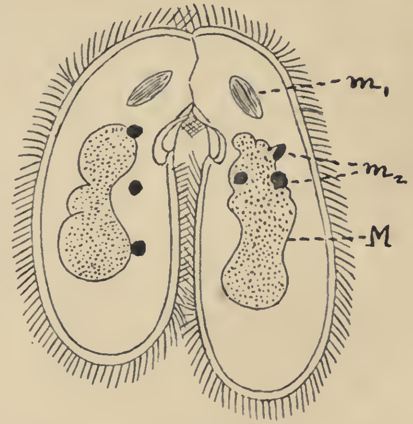


Fig. 38.

A stage in conjugation of *Colpidium colpoda* just before the formation of the migratory and stationary micronuclei. *M*, meganucleus ; $m_1$, the sexual nucleus ; $m_2$, the three nuclei undergoing degeneration. (After Hoyer.)

Returning to the earlier stages of conjugation, and tracing the fate of the original meganuclei, we find that, apart from minor changes in the arrangement of the chromatin network, the meganuclei do not seem to be affected by the union of the two individuals. Later on, however, they become irregular in outline

(III., V.), break up into lumps (VI.), into smaller droplets, and ultimately disintegrate (X.) and disappear (XI.).

The changes which take place in the cytoplasm during conjugation have not yet been followed in detail. There can be little doubt that an interchange of molecules of cytoplasm between the two individuals does occur, but it is quite impossible to tell whether the mixing of the two cytoplasms is or is not complete.

In the accounts given of the conjugation of the Ciliata, it is stated that the meganucleus plays a perfectly passive rôle until its disintegration begins.

In *Spirochona* the meganuclei fuse during conjugation; and in *Dendrocometes* the meganuclei come in contact during conjugation, but subsequently separate (Fig. 39).

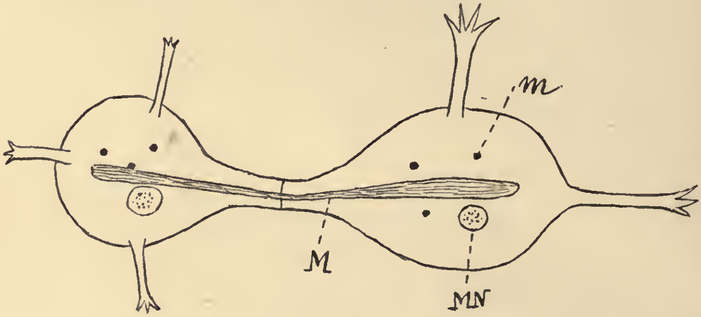


FIG. 39.

Reconstruction of a series of sections through a pair of conjugating *Dendrocometes*, showing a temporary fusion of the two meganuclei (*M*), at the conclusion of the process. *MN*, the new meganucleus; *m*, the three new micronuclei. (Original.)

In those species which normally possess more than one micronucleus the process is rather more complicated.

In *Paramoecium aurelia* the two micronuclei which are normally present in each individual divide twice, giving rise to eight nuclei, of which number seven degenerate and one remains as the sexual nucleus. After the conjugation of the migratory and stationary nuclei, the cleavage nucleus of each individual divides twice, and of the four nuclei thus formed, two directly give rise to meganuclei and the remaining two divide again to give rise to the two micronuclei in each of the daughter individuals formed by the first fission.

In *Dendrocometes* there are usually three micronuclei in each individual. At the commencement of conjugation all three micronuclei enlarge and undergo mitosis (Fig. 40), but not simultaneously. Of the six nuclei thus formed, five degenerate and one passes down the junction and forms the sexual nucleus.

In *Bursaria truncatella* there are, according to Prowazek, normally 16-18 micronuclei in each individual, which give rise to no less than

66-78 descendant nuclei during conjugation, but they all degenerate except one, which alone forms the sexual nucleus (Fig. 60).

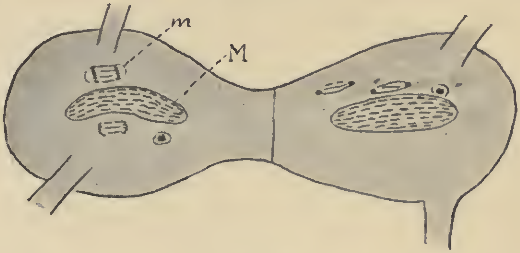


FIG. 40.

Reconstruction of a series of sections through a pair of *Dendrocometes* at the beginning of conjugation. *M*, the meganucleus. *m* points to one of the micronuclei in the process of mitosis. One of the three micronuclei in each individual has not begun to divide, but it is much larger than the micronuclei of individuals that are not conjugating. (Original.)

In the VORTICELLIDAE there is a further modification of the process. The micronucleus of the female divides twice, to form four nuclei, and of these, three degenerate; the micronucleus of the male, on the other hand, divides three times, to form eight nuclei, of which seven degenerate (Fig. 43). Only one cleavage

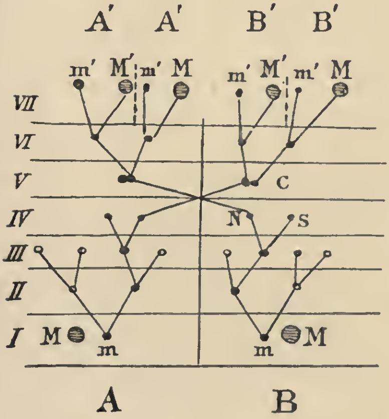


FIG. 41.

Diagram I., to illustrate the nuclear changes during conjugation of two Holotrichans, *A* and *B*. *M*, meganucleus; *m*, micronucleus; *N*, migratory nucleus; *S*, stationary nucleus; *C*, cleavage nucleus; *M'*, the meganucleus, and *m'*, the micronucleus of the individuals, *A' A'*, *B' B'*, formed by the first fission after conjugation.

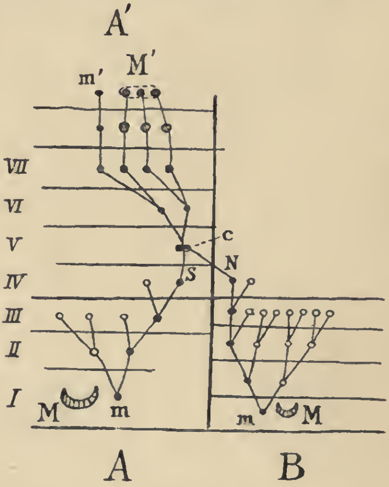


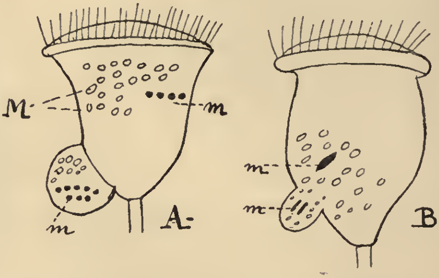
FIG. 42.

Diagram II., to illustrate the nuclear changes during the conjugation of a female (*A*) and a male (*B*) *Voticella*. *M*, meganucleus; *m*, micronucleus of *A* and *B*; *S*, stationary sexual nucleus; *N*, migratory sexual nucleus; *c*, cleavage nucleus; *M'*, the meganucleus formed by the fusion of three nuclei; and *m'*, the micronucleus of the regenerated female *A'*.

nucleus is formed, namely, the one in the female individual. The male shrivels and dies. The cleavage nucleus divides twice, and three of the nuclei enlarge and subsequently fuse to form the new meganucleus, whilst the remaining one forms the new micronucleus.

FIG. 43.

Two stages in the conjugation of *Vorticella monilata*. In *A* the micronucleus of the female has given rise to four nuclei, the micronucleus of the male to eight nuclei; the meganuclei (*M*) in both have disintegrated. In *B*, which represents a later stage, the cleavage nucleus has been formed in the female; in the male the migratory and stationary sexual are close together, but do not fuse. (Diagrammatic drawings after Maupas. The ciliated discs are actually retracted during these stages.)



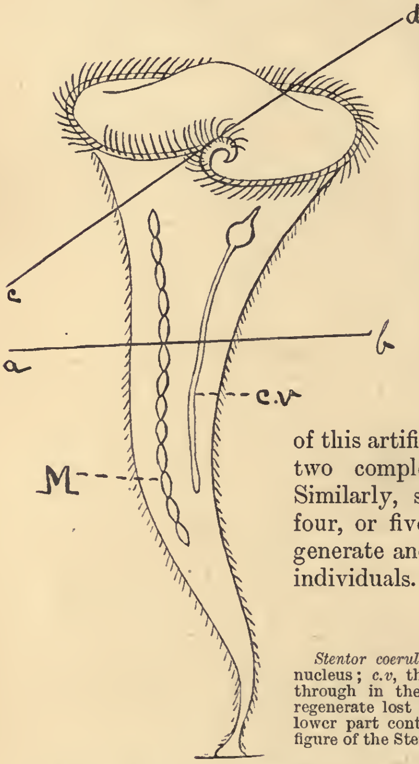


FIG. 44.

*Stentor coeruleus*, Ehrb. *M*, the long moniliform meganucleus; *c.v*, the contractile vacuole. If the animal is cut through in the plane *a-b*, both portions will survive and regenerate lost parts; if it be cut in the plane *c-d*, only the lower part containing the meganucleus will survive. (The figure of the Stentor after Saville Kent.)

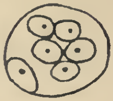
REGENERATION. — Several series of experiments have now been recorded which prove that the Ciliata possess very considerable powers of the regeneration of lost parts. If, for example, a *Stentor* be cut into two parts transversely, the upper part will, in a little while, close up the wound, and eventually form a base similar in all essential respects to the parts that are lost; the lower portion will, on the other hand, produce a new spiral disc and a new mouth. Thus, as a result of this artificial section of a single individual, two complete individuals are produced. Similarly, sections of the body into three, four, or five pieces may be made, which regenerate and give rise to new and complete individuals. There are limits, however, to this power of regeneration. If a section be made through a *Stentor* in the plane of the line *c-d* in Fig. 44, it will be found that the segment containing the meganucleus will regenerate the lost part; the segment which contains no portion of the meganucleus, however, will degenerate and die. Further experiments that have been made on *Stentor*, on *Stylonychia*, and other forms prove that a portion of the meganucleus plays an essential part in the regeneration of the segments, and that in all cases the detached parts of an infusorian that are devoid of meganucleus, however large they may be, degenerate and die without repairing their injuries. The nucleated fragments, on the other hand, are capable of regenerating lost parts even when they are exceedingly small, but a limit of size may be reached, which in the case of *Stentor* is said to be 80 $\mu$ in diameter (Lillie), below which even nucleated fragments die.

There is very little evidence upon the history of the micronuclei in these experiments. Le Dantec, however, states that segments which contain no micronuclei are capable of regenerating lost parts, and that in such cases a new micronucleus is formed by the meganucleus.

## The Morphology of the Heterokaryote Body.

The generally accepted view that the body of one of these animals is strictly unicellular requires some modification unless our definition of an animal cell is to be widely extended. In the Metazoan body we can recognise two classes of cells—the somatic cells, which perform the general functions of the body; and the germinal cells, which are alone concerned with reproduction. We can also recognise two classes of nuclei in the same manner—the somatic nuclei and the germinal nuclei. In the Metazoan body there is a large number of somatic cells, and each of them contains, as a general rule, a single somatic nucleus, and similarly each of the many germinal cells contains, usually, a single germinal nucleus.

Many instances could be quoted (striated muscle, nerve fibres), however, in which the cell outlines of both somatic and germinal cells are ill-defined or absent, so that the tissues become indistinguishable from multinuclear plasmodia. There can be no reason, however, for calling such tissues unicellular tissues. The actual number of cells composing the Metazoan body varies enormously, and it is not inconceivable that an animal may have existed (Fig. A) with only one somatic cell and one or two germinal cells, and for protection the germinal cells (*m*, *m*) might be within instead of outside the larger somatic cell (M).[1]



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[1] Parallel examples of this may be found in the spermatogenesis of Spongilla, Helix, Cossus, etc., in which the germinal cells are within the blastophoral cell.

If, however, in such an animal the limits of somatic and germinal cytoplasm were indistinguishable (Fig. B), we should have an organism precisely similar in its essential features to one of the Heterokaryota, and just as the hypothetical form is strictly bicellular or tricellular, so is the Heterokaryote, strictly speaking, not unicellular, but bicellular or tricellular, etc., according to the number of micronuclei it possesses.

The matter is, however, to a certain extent a question of nomenclature. If it is considered to be desirable to include in the term, "cell," everything that is enclosed by the outline of a cytoplasmic unit, then the Heterokaryota may be called unicellular; but the definition of a cell must be extended so as to include examples in which the cytoplasm includes nuclei of two or more distinct characters.

The differences between the meganucleus and the micronucleus in the Heterokaryota are very pronounced.

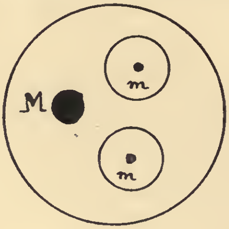

Fig. A.

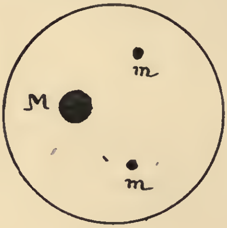

Fig. B.

The meganucleus is undoubtedly somatic in function. The experiments mentioned on p. 392 prove that it is essential for the process of the repair of injuries and for the restoration of parts that have been lost; the changes in the structure of its granules observed during assimilation and starvation point to its important relations with the processes of digestion, whilst the changes in its shape and position, during the somatic life of the individual, indicate its continued functional activity during this period.

Speaking generally of the meganucleus of the Heterokaryotes, it may be remarked that, as compared with other nuclei, it exhibits an extraordinary variety of form. It may be spherical, oval, band-like, moniliform, dumb-bell shaped, double, or scattered in numerous small fragments.

The exact meaning of this may be obscure, but it is quite consistent with the facts to believe that its peculiar shapes are associated with the important somatic functions, over which it exercises some essential control.

Whilst it is thus clear that the meganucleus is somatic in function, it is none the less evident that the micronucleus is not.

During the whole of the somatic life, that is to say, between the acts of fission and conjugation, the micronuclei remain extremely small, the chromatin being concentrated into an extremely minute granule, and there can be little doubt that they are in a condition of rest.

During conjugation, however, the relative activity of the two nuclei is reversed. The micronuclei enlarge, divide by mitosis, and show other signs of extreme activity. It is the products of the division of micronuclei alone that fuse to form the cleavage nuclei. The meganuclei, on the other hand, degenerate and disappear. The evidence, therefore, is conclusive that the meganucleus is a somatic nucleus, and may be compared with the nuclei of the cells of the body of a Metazoon, and that the micronucleus is a sexual nucleus, and can be only compared with the nuclei of the sexual cells of the Metazoon.

There is very little evidence, however, that there is allocated to each micronucleus in the Infusorian's body a specialised part of the cytoplasm, as there is in the Metazoon. There is, in other words, evidence of a sexual nucleus, but very little evidence of sexual cytoplasm. If we assume that such sexual cytoplasm does exist, and that during the act of conjugation the sexual cytoplasm of the two individuals mingles, the parallelism between the sexual act of the Infusoria and that of the Metazoa is established.

But without making any assumption whatever, it is clearly erroneous to compare the conjugation of two Infusorians with the conjugation of an ovum and a spermatozoon. The degeneration of the meganucleus after or during conjugation clearly proves that the Infusorian is something more than a mere sexual cell or gamete. It is only a part, and a very small part too, of the whole body of the Infusorian that functionally conjugates, the remainder is only accessory to the act. It is therefore only misleading to call the stalked *Vorticella* a megagamete and the free-swimming individual that becomes attached to it a microgamete. These individuals have all the essential features of female and male individuals, and the act that they perform is essentially an act comparable to the copulation of the Metazoa. Similarly, the conjugating individuals of the Holotricha ought not to be called Isogametes, but hermaphrodite individuals.

An important and interesting question then arises as to the individuality of the Infusoria before and after conjugation. The destruction of the old somatic nucleus during conjugation is proved, but there is also evidence of a less satisfactory nature that the somatic cytoplasm undergoes regeneration after the act. If it be assumed that the old somatic cytoplasm is gradually replaced by the conjoint sexual cytoplasm of the two conjugates, then the individuality of the Infusorian before and after conjugation is not identical. It is clear that there is partial somatic death during conjugation; it is not clear, however, that there is complete somatic death. It is to the elucidation of this important question that we may look with confidence to future investigations.

## CLASS CILIATA, EHRB.

| | Examples of a Genus. |
|---|---|
| ORDER HOLOTRICHA. | |
| Sub-Order **Gymnostomata.** | *Prorodon.* |
| Sub-Order **Hymenostomata.** | *Paramoecium.* |
| ORDER HETEROTRICHA. | |
| Sub-Order **Polytricha.** | *Stentor.* |
| Sub-Order **Oligotricha.** | *Ophryoscolex.* |
| ORDER HYPOTRICHA. | *Stylonychia.* |
| ORDER PERITRICHA. | *Vorticella.* |

The **Ciliata** may be most conveniently divided into four orders—the HOLOTRICHA, the HETEROTRICHA, the HYPOTRICHA, and the PERITRICHA. Of these orders the HOLOTRICHA undoubtedly contain those genera which are the most primitive in their anatomical characters, the other three orders contain genera which have probably reached their present condition on independent lines of evolution from a common holotrichous ancestor.

### ORDER **Holotricha**, Stein.

The order HOLOTRICHA includes those free-swimming Ciliata in which the cilia are all of approximately equal length and thickness. There are never any structures of the nature of cirri.

The order is divided into two sub-orders—(1) the GYMNOSTOMATA, in which the mouth is closed in the intervals between the acts of the ingestion of food; and (2) the HYMENOSTOMATA, in which the mouth is always open and provided with an undulating membrane.

#### SUB-ORDER GYMNOSTOMATA, Bütschli.

The GYMNOSTOMATA are usually of small size, rarely exceeding $\frac{1}{3}$ mm. in length. Several of the genera (*Holophrya*, *Enchelys*, etc.) occur both in the sea and in the fresh-water, others are found only in fresh-water (*Prorodon*, *Lacrymaria*, *Didinium*, etc.), others only in sea-water (*Stephanopogon*, *Onychodactylus*), and others are parasitic (*Bütschlia* in the stomach of Ruminants).

In the more primitive forms (*Holophrya*, *Enchelys*) the mouth is a simple passage from the medulla to the exterior, situated at the anterior extremity of the body. In several forms the passage is kept open for the greater part of its length by a palisade arrangement of stiff rods commonly called the pharynx, but the mouth itself can be closed by the cortex contracting over the anterior end of the pharynx (*Prorodon*, *Coleps*).

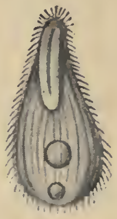

Fig. 45.

*Spathidium lieberkühnii*, Bütschli, showing the elongated, slit-like mouth above, the nucleus in the centre, and the contractile vacuole below. (After Bütschli.) × 220.

The position of the mouth is by no means constant in the group. In *Spathidium* (Fig. 45) it is somewhat elongated, and situated just behind the anterior end of the body.

In *Nassula* it is situated at a distance of about one-third of the length from the pointed anterior end of the body.

In *Dileptus* and *Trachelius* (Fig. 7) there is a long narrow lobe in front of the mouth.

The cilia are, in the most primitive forms (*Holophrya*, etc.), evenly distributed over the surfaces of the body; in some of these, however, the cilia which are arranged in a circlet round the mouth are a trifle longer and thicker (*Lacrymaria*) than those on the general surface. In the larger forms it may be observed that the cilia are arranged in parallel rows running longitudinally down the body or slightly curved like the rifling of a firearm. In *Didinium* the cilia are confined to two fine horizontal bands, and in the parasitic *Bütschlia* and others the cilia occur in irregular ridges and tufts.

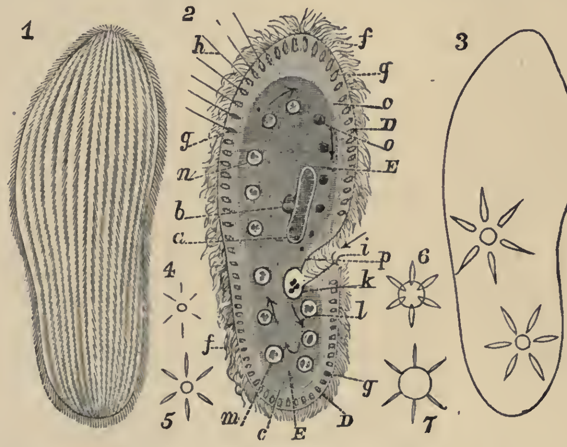

Fig. 46.

1, Surface view of a Holotrichous Ciliate, showing the disposition of the cilia in longitudinal rows. 2, diagrammatic optical section of the same, showing all structures except the contractile vacuoles; *a*, meganucleus; *b*, micronucleus; *c*, cortex; *D*, pellicle; *E*, medulla; *f*, cilia; *g*, trichocysts; *h*, filaments ejected from the trichocysts; *i*, mouth; *k*, drop of water containing food particles about to sink into the medulla and form a food vacuole; *l*, *m*, *n*, *o*, food vacuoles, the successive order of their formation corresponding to the alphabetical sequence of the letters; *p*, pharynx. 3, outline of a *Paramoecium* to show the form and position of the contractile vacuoles. 4-7, successive stages in the formation of the contractile vacuoles. (From Lankester.)

In the remarkable genus *Actinobolus* there are a number of retractile processes called the tentacles projecting in a radiating manner from the body-wall, which give the animal a superficial resemblance to a Heliozoon (Fig 48).

In *Ileonema* there is a single flagellate process at the anterior end of the body which is capable of being completely withdrawn (Fig. 49).

Nearly all the Gymnostomata are provided with trichocysts. They are situated either in special aggregations round the mouth, in which case they are regarded as weapons of offence; or scattered over the general surface of the body, in which case they are regarded as weapons of defence.

The meganucleus is frequently spherical or oval in shape, but it is sometimes elongated, horse-shoe-shaped, moniliform, jointed, segmented, or fragmented. The micronucleus of a considerable number of genera has not yet been discovered, but in others there can be no doubt of the existence of one (*Chilodon*) or more (*Dileptus*) micronuclei.

The genera of Gymnostomata are divided into families by Schewiakoff as follows:—

Family Holophryina, Perty. *Holophrya*, Ehrb. Of very simple structure, with a terminal mouth provided with only a very rudimentary pharyngeal apparatus. They form spherical cysts surrounded by a gelatinous case in which an enormous number of young are produced by rapid and repeated fissions (Figs. 36 and 47). 0·4.[1] Freshwater and marine, sometimes parasitic on freshwater fish. *Urotricha*, Clap. and L. Exceedingly minute forms distinguished by the presence of a single long straight bristle at the posterior end. 0·04. Freshwater. *Enchelys*, Hill. Anterior and posterior ends somewhat attenuated, but in other respects similar to preceding genera. Well-developed trichocysts. ·02-·2. Freshwater and marine. *Spathidium*, Duj. Body flask-shaped. Mouth ventral at the anterior end, long and slit-shaped. 0·4. Freshwater. (Fig. 45.) *Cranotheridium*, Schew. With an elaborate pharyngeal armature. Numerous micronuclei and a single meganucleus. 0·17. Freshwater. *Lagynus*, Quenn. Bottle-shaped, with a pharynx surrounded by numerous trichocysts. 0·18. Marine and freshwater. *Trachelophyllum*, Clap. and L. Similar to the preceding genus, but with the body a little more flattened. 0·2. Marine and freshwater. *Lacrymaria*, Ehrb. Elongated, extremely contractile forms. Anterior end shaped like a bottle cork and surrounded by four or five bands of long cilia. 0·8. Freshwater and marine. *Trachelocerca*, Ehrb. Very elongated and contractile forms. Mouth surrounded by four lappets or lobes. Some-

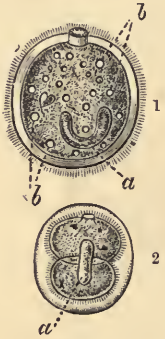

Fig. 47.

*Holophrya multifiliis*, Fouquet. 1, free-swimming condition. 2, encysted condition with protoplasm undergoing its first transverse fission. *a*, meganucleus; *b*, *b*, contractile vacuoles. × 120.

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[1] These figures refer to the average length of the genera in millimetres.

times reach a total length of 3 mm. Marine. *Prorodon*, Ehrb. Usually spherical in form, with a well-developed pharyngeal armature. 1 mm. Freshwater. (Fig. 8.) *Perispira*, Stein. Bands of cilia arranged in a spiral manner. 0·05. Stagnant freshwater. *Chaenia*, Quenn. An elongated and contractile form with a special group of long cilia at the anterior attenuated extremity. 0·25. Marine.

Family Actinobolina, Stein. *Actinobolus*, Stein (Fig. 48). Spherical in shape, provided with a uniform covering of long cilia. The most remarkable feature of this genus is the power they possess of protruding a considerable number of long, needle-shaped protoplasmic processes or tentacles, each armed at its extremity with a large trichocyst. 0·1. Freshwater. *Ileonema*, Stokes. Flask-shaped, with a long prehensile appendage springing from the oral extremity (Fig. 49). 0·2. Freshwater.

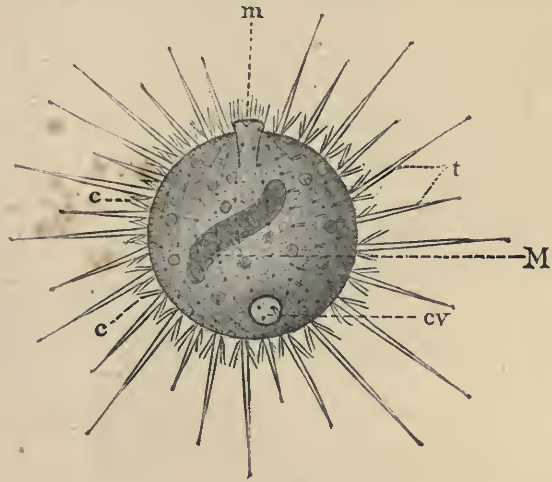

Fig. 48

*Actinobolus radians*, Stein, with the peculiar tentacles (*t*, *t*) fully extended. Each tentacle bears at its extremity a trichocyst. *m*, mouth; *M*, meganucleus; *c.v*, contractile vacuole; *c*, *c*, cluster of cilia at the insertion of the tentacles. (After Schewiakoff.) × 400.

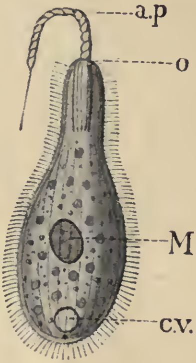

Fig. 49.

*Ileonema dispar*, Stokes. *M*, meganucleus; *o*, mouth; *a.p*, anterior prehensile appendage; *c.v*, contractile vacuole. (After Schewiakoff.) × 300.

Family Colepina, Ehrb. *Plagiopogon*, Stein. Without carapace. Very small. Freshwater. *Coleps*, Nitzsch. Body covered by a complicated carapace (Fig. 5). 0·05. Freshwater. *Tiarina*, Bergh. Similar to the above, but with a pointed posterior extremity. Marine. *Stephanopogon*, Entz. Slightly elongated forms, flattened on ventral side, with a large horse-shoe meganucleus. 0·07. Marine.

Family Cyclodinina, Stein. *Dinophrya*, Bütschli. Cylindrical in form, with a pointed posterior extremity. 0·1. Freshwater. *Didinium*, Stein (Fig. 74). Cylindrical in form, with a conical peristome. Cilia restricted to a few circular bands. Mouth capable of extraordinary dilatation. 0·2. Freshwater. *Mesodinium*, Stein. Cilia reduced to a single band, very long and strong. 0·04. Marine and freshwater.

Family Prorotrichina, Bütschli. *Bütschlia*, Schuberg. Very minute cilia covering the general surface of the body, but a special perioral crown of longer cilia, and a tuft of the same at the posterior extremity. 0·06. Rumen of Ruminants. The genera *Blepharocodon*, *Blepharoprosthium*, and *Blepharosphaera* described by Bundle from the coecum of the horse are perhaps members of this family.

Family Amphileptina, Bütschli. *Amphileptus*, Clap. and L. The anterior end pointed, and on the ventral side of this a long slit-like mouth. Meganucleus in two or four pieces. 0·2. Marine, freshwater, and in infusions. *Lionotus*, Wrzs. Similar to above, but rather more elongated and flattened. 0·4. Marine and freshwater. *Loxophyllum*, Duj. Similar to above, with the body more flattened and contractile. 0·04. Marine and freshwater. *Loxodes*, Ehrb. A creeping, spindle-shaped form, with several meganuclei and micronuclei. 0·5. Freshwater.

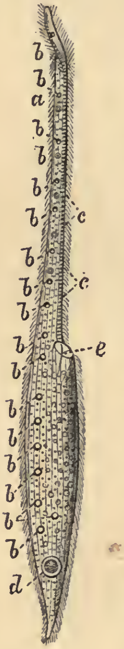

Fig. 50.

*Dileptus anser*, O.F.M. (=*Amphileptus gigas* of Claparède and Lachmann). *b*, *b*, contractile vacuoles; *c*, *c*, trichocysts on the ventral side of the proboscis; *d*, a food vacuole; *e*, mouth. × 100.

Family Trachelina, Stein. *Trachelius*, Clap. and L. (Fig. 7). Spherical in form, with a short proboscis in front of the round mouth. 0·4. Freshwater. *Dileptus*, Duj. (Fig. 50). Very elongated and contractile, with a long proboscis armed with trichocysts in front of the round mouth. Meganucleus moniliform. 1 mm. Marine and freshwater.

Family Nassulina, Bütschli. *Nassula*, Ehrb. Oval forms with a long, complicated pharyngeal armature. Mouth on the ventral side, a short distance from the anterior end. Frequently red, blue, or brown in colour. 0·3. Freshwater and marine.

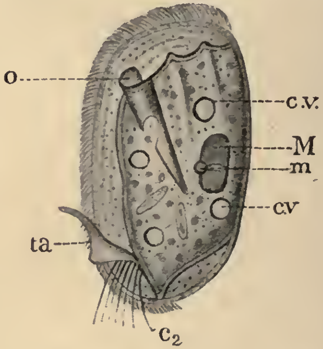

Fig. 51.

*Dysteria armata*, Huxley. *o*, mouth; *M*, meganucleus; *m*, micronucleus; *c.v*, *c.v*, four contractile vacuoles; $c_2$, anal cirri; *ta*, caudal appendage. (After Schewiakoff.) × 400.

Family Chlamydodonta, Stein. *Orthodon*, Gruber. Cilia on ventral side much longer than on the dorsal side. Mouth on the right side. 0·26. Marine and freshwater. *Chilodon*, Ehrb. Oval in outline. Strongly compressed dorso-ventrally. 0·3. Very common in infusions. *Chlamydodon*, Ehrb., 0·12, marine; *Scaphidiodon*, Stein, 0·1, marine; *Phascolodon*, Stein, 0·09, freshwater; and *Opisthodon*, Stein, 0·18, freshwater, are all closely related to *Chilodon*.

Family Dysterina, Clap. and L. *Aegyria*, Clap. and L. Body usually ventrally folded. Cilia apparently confined to the ventral side.

0·15. Marine. *Dysteria*, Huxley (Fig. 51). Body somewhat resembling a mussel in shape, with a very restricted ventral side which alone bears cilia. There is a remarkable caudal appendage on the ventral side. The dorsal side is smooth and ribbed. 0·15. Marine and freshwater. *Trochilia*, Duj. 0·035. Freshwater and marine. *Dysteropsis*, Roux. Lacustrine.

Family ONYCHODACTYLINA, Entz. *Onychodactylus*, Entz. The body bears at the posterior end a little conical appendage in the form of a tail, at the extremity of which is the anus. The colour is yellow or blue. 0·2. Marine.

### SUB-ORDER HYMENOSTOMATA, Delage.

The HYMENOSTOMATA include a large number of forms that occur in infusions such as *Loxocephalus*, *Colpidium*, and *Colpoda*, from which the name of the Class Infusoria was derived. Some of them are internal parasites such as the OPALININA and ISOTRICHINA. Others are free-swimming in pure water. They vary in size from the minute *Cyclidium*, ·03 mm., and *Loxocephalus*, ·06 mm., to the elongated parasite *Discophrya*, which is sometimes 2 mm. in length.

The mouth is in some cases at the anterior extremity of the body, but more usually it is situated near the middle of one side. In such forms as *Isotricha* it is doubtful which end of the body is correctly called anterior. According to Bütschli and others the mouth is situated at the posterior end, and the animal swims with the anterior end foremost. Others consider that the mouth is at the anterior end, and that the animal habitually swims backwards.

The mouth is usually situated at the bottom of an elongated, gutter-like peristomial depression, and opens into a short oesophageal tube. This tube, however, is never supported by a palisade of rods. In many forms, and perhaps in all of them, there is a small undulating membrane at the margin of the mouth—hence the name Hymenostomata. Sometimes there is in addition to this one or two very delicate membranes (*Pleuronema*) at the margins of the peristomium which it is convenient to distinguish as the lips (Fig. 52). Trichocysts are usually present. There is generally a single spherical or oval meganucleus accompanied by one or two micronuclei. In *Frontonia* there are several micronuclei. In *Anoplophrya* (Fig. 30) there is an elongated meganucleus and in *Opalinopsis* (Fig. 55) an irregular band-like meganucleus at first, which in the older forms breaks up into a number of fragments. In *Opalina* there are several spherical meganuclei, and probably a greater number of micronuclei (Fig. 25).

Reproduction is effected by simple transverse fission. In *Leucophrys* there is a resting stage during which the animal becomes spherical in shape, but does not secrete an envelope. During this stage the body divides into thirty-two small individuals. In *Ophryoglena*, *Colpoda*, and *Glaucoma* cysts are formed. The kidney-shaped cysts of *Paramoecium* have recently been figured by Lindner. The body of *Opalina*, after it has reached a certain stage of growth, divides by fission several times, until the fragments contain only two or three nuclei. Each fragment then becomes encased in a spherical cyst. This is passed into the water, and if it is then swallowed by a tadpole, gives rise to a uninucleated spore which absorbs nourishment and grows. As it grows the nucleus divides, and so the large multinucleate form from which it sprang is reattained (Figs. 53 and 54).

The Hymenostomata are arranged by Schewiakoff as follows:—

Family Chilifera, Bütschli. *Blepharostoma*, Schew. With very long peribuccal cilia. ·015. Freshwater. *Dichilum*, Schew. With right and left lips, the latter rudimentary. 0·03. Freshwater. Australia. *Trichospira*, Roux. Freshwater. *Dallasia*, Stokes. Dorsal side concave, ventral side convex. Very large mouth, just behind the anterior extremity. Two undulating membranes. Swims on the concave dorsal side. 0·14. Freshwater. *Plagiocampa*, Schew. A lip on the left side only. A border of labial cilia on the right. 0·04. Freshwater. Australia. *Uronema*, Duj. Oval in form, slightly compressed. Convex on the dorsal side. Flat on the ventral side, with an excavation in the buccal region. Provided with a long caudal cilium. 0·07. Freshwater. *Stegochilum*, Schew. Pharynx absent. Well-developed labial membrane. 0·07. Freshwater. Australia. *Cryptochilum*, Schew. *Leucophrys*, Ehrb. Body compressed. Provided with a large, tongue-shaped, undulating membrane. 0·25. Freshwater. *Leucophrydium*, Roux. *Monochilum*, Schew. In the form of an elongated cylinder. *Loxocephalus*, Kent. Undulating membrane doubtful. A single long cilium at posterior end, also a row of specially long cilia on the right side. 0·05. Freshwater and in infusions. *Chasmatostoma*, Engelmann. Kidney-shaped. 0·06. Freshwater. *Glaucoma*, Ehrb. Oval in form, but slightly flattened. Cilia evenly distributed. 0·1. Freshwater, but principally found in infusions. *Urozona*, Schew. Only the middle part of the body furnished with cilia, which form a thick band encircling the body. 0·03. Freshwater. *Colpidium*, Stein. Oval or kidney-shaped. A large mouth situated some distance behind the anterior extremity on the ventral side of the body. Cilia evenly distributed. 0·12. This genus and the next (*Colpoda*) very common in freshwater infusions. Colpidium also occurs in marine infusions. *Colpoda*, Müller. Similar to *Colpidium*, but more definitely kidney-shaped. The twist in the rows of cilia at the anterior end is from left to right, the opposite of that in *Colpidium*. 0·1. Very common in hay infusions. *Frontonia*, Clap. and L. Large cylindrical bodies or pointed posteriorly. On the right border of the mouth there is a ciliated stripe, free from trichocysts. Colourless or green with Zoochlorellae, sometimes provided with black or brown pigment. 0·35. Freshwater and marine. *Disematostoma*, Lauterb. *Philaster*, Fabre Dom. *Ophryoglena*, Clap. and L. 0·5. Freshwater. *Blepharocorys*, Bundle. Coecum of the horse.

Family Microthoracina, Wrzesniowski. *Cinetochilum*, Perty. This animal appears to swim upside down. During progression the extremity which bears the mouth is posterior. It is provided with two vibrating lips, of which the right is larger than the left. 0·04. Freshwater. *Microthorax*, Engelmann. The mouth turned more to the right side than in the preceding genus. 0·06. Freshwater. *Trichorhynchus*, Balb. One end is drawn out into a conical papilla armed with long cilia. Bütschli regards this end as posterior. 0·04. Freshwater. Tuamotu. *Ptychostomum*, Stein. 0·1. Occurs in the intestine of Oligochaeta. *Ancystrum*, Maupas. Ovoid in form, with a series of long cilia on the ventral border. 0·07. In the pallial cavity of marine Pelecypoda.

Family Paramoecina, Duj. *Paramoecium*, Stein. There is a minute undulating membrane on the dorsal side of the pharynx. Trichocysts usually occur over the whole surface of the body. One or two contractile vacuoles. One or two micronuclei. Up to 0·25 in length. Very common. Freshwater and marine. (Fig. 46.)

Family Urocentrina, Clap. and L. *Urocentrum*, Nitzsch. The ciliation of the body reduced to two broad zones. The peristome extends from the posterior edge of the anterior zone to the hind end of the body. 0·1. Marine and freshwater.

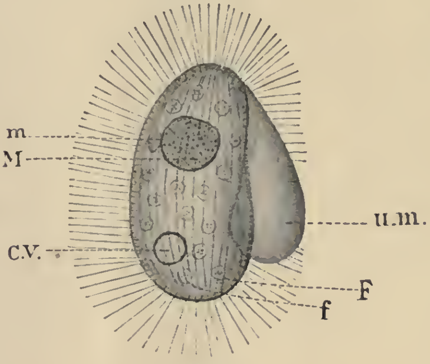

Fig. 52.

*Pleuronema chrysalis*, O.F.M. *M*, meganucleus; *m*, micronucleus; *u.m*, the large right undulating lip; *f*, *F*, food particles; *c.v*, contractile vacuole. (After Schewiakoff.) × 400.

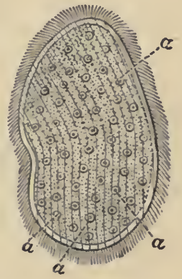

Fig. 53.

*Opalina ranarum*, Purkinje. *a*, *a*, the meganuclei. (From Lankester, after Zeller.) × 100.

Family Pleuronemina, Bütschli. *Lembadion*, Perty. The peristome is a deep groove extending from the anterior end of the body almost to the posterior. It is covered by two large undulating lips. A small undulating membrane also occurs on the right side of the peristomial groove. *Pleuronema*, Duj. (Fig. 52). A very large peristome with a large right undulating lip. Springing movement. 0·03. Marine and freshwater. *Lembus*, Cohn. An elongated form with two undulating lips. 0·1. Marine infusions. *Cyclidium*, Clap. and L. Very similar to *Pleuronema*, but smaller. 0·03. Freshwater and marine. *Cristigera*, Roux. Freshwater. *Pleurocoptes*, Wallengren, occurs on Hydractinia.

Family Isotrichina, Bütschli. *Isotricha*, Stein. Spherical forms with a mouth situated at the posterior (?) end. A well-marked anus situated anteriorly. Numerous minute contractile vacuoles scattered through the protoplasm. 0·16. Rumen of the Artiodactyla. *Dasytricha*, O. Schuberg. No anus. Lines of cilia rather more spirally arranged than in *Isotricha*. 0·1. Rumen of Artiodactyla. *Paraisotricha*, Fiorent. Coecum of the horse.

Family Opalinina, Stein. Without a mouth. *Anoplophrya*, Stein. Oval to elongated in shape, slightly twisted on its axis. A row of contractile vacuoles along one border. 0·9. Digestive canal of Annelids and Gastropods, and in the blood of some Crustacea. (Fig. 30.) *Hoplitophrya*, Stein. Anterior end of the body formed like a sucker and provided with two hooks. A long tubular contractile vacuole. 0·9. Intestine of Planarians and Oligochaeta. *Discophrya*, Stein. A large sucker-like anterior end without hooks. 2 mm. Digestive canal of Planaria and Amphibia. *Opalina*, Purkinje (Figs. 25, 53, 54). The most aberrant of all the Hymenostomata. No contractive vacuoles. Numerous meganuclei. 0·1. Rectum and occasionally the bladder of several Anura. *Opalinopsis*, Foettinger (Fig. 55). Elongated in form, with a swollen anterior end. In the young forms a band-like meganucleus, which later breaks up into a large number of irregular fragments. 1·5. Liver and venous appendages of various Cephalopoda.

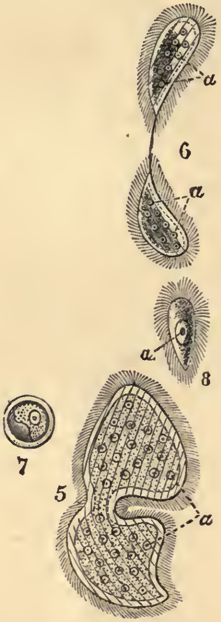

Fig. 54.

Reproduction of *Opalina ranarum*. 5, a specimen in process of binary fission; 6, the same; the process of fission has now reduced the individuals to a relatively small size; 7, smallest fission produced fragment encysted, expelled from the frog in this state and swallowed by a tadpole; 8, young uninucleate individual which has emerged from the cyst within the tadpole and will now multiply its nuclei and grow to full size. (After Zeller.)

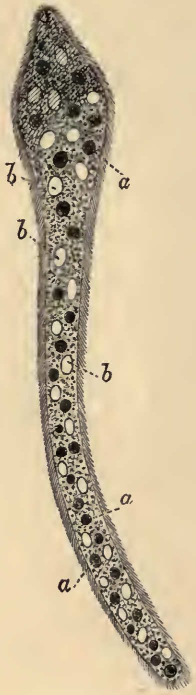

Fig. 55.

*Opalinopsis sepiolae*, Foett, a mouthless Holotrichan from the liver of the squid. *a*, *a*, fragments of the meganucleus which in the younger stages is a continuous rod or band. *b*, *b*, non-contractile vacuoles. × 100.

### ORDER **Heterotricha**, Stein.

This order includes those Ciliata in which there is a special adoral zone, armed with specialised long or thick cilia, supported by a delicate protoplasmic ridge or membranella, and usually spiral in form.

The Order is divided into two Sub-orders:—

Sub-order POLYTRICHA.
Sub-order OLIGOTRICHA.

The sub-order POLYTRICHA includes those HETEROTRICHA in which the general surface of the body is covered with rows of short cilia. The longer cilia are usually confined to the adoral zone, but may also occur in the form of a tuft (*Metopus*) at the posterior end of the body. The form of the body may be spherical (*Bursaria*), oval (*Condylostoma*), rod-like (*Spirostomum*), or trumpet-shaped (*Stentor* and *Folliculina*). Most of the genera are permanently free-swimming, but some are occasionally (*Stentor*) or usually (*Folliculina*) sedentary in habit. In *Bursaria*, *Balantidium*, and others the mouth is at the anterior end of the body. In *Chonchophthirus* and *Spirostomum* it is near the middle, whilst in *Plagiotoma* it is situated nearer to the posterior than to the anterior end.

This sub-order contains some of the largest Ciliata. The elongated *Spirostomum* may be 3 mm. in length, *Bursaria* is occasionally 1·5 mm. in diameter, and *Stentor* and *Folliculina* 1 mm. in length in the extended condition. Some genera (*Stentor*, *Folliculina*) have considerable powers of contracting and extending the body. In *Spirostomum* the contraction is spiral. Trichocysts have not yet been discovered in any POLYTRICHA. The meganucleus is oval in *Nyctotherus*, *Blepharisma*, *Balantidium*, and others. In *Spirostomum* it is oval at one time and at others it becomes very elongated and moniliform. In *Stentor* it is moniliform (Fig. 44). In *Plagiotoma* and *Bursaria* it is elongated. In *Balantidium* and others only one micronucleus has been seen; but in *Stentor*, *Bursaria*, *Spirostomum*, etc., there are numerous micronuclei.

The POLYTRICHA contain the following families:—

Family PLAGIOTOMINA, Clap. and L. *Conchophthirus*, Stein. The adoral zone represented by a row of long cilia on the anterior border of the peristome. 0·2. Ectoparasitic on the mucus of several fresh- and salt-water Pelecypoda. Also found in the body-cavity of various species of Actiniaria. *Plagiotoma*, Duj. Slightly contractile. Meganucleus a long twisted band. 0·4. Parasitic in the intestine of earthworms. *Nyctotherus*, Leidy. This is regarded as a sub-genus of *Plagiotoma* by Bütschli. It is distinguished from it by its reniform shape and by the sausage-shaped or oval meganucleus. 0·3. Parasitic in the intestines of Anura and various insects and myriopods. (Fig. 56.) *Blepharisma*, Perty. Very similar to *Plagiotoma*, but not parasitic. 0·4. Freshwater. *Metopus*, Clap. and L. Oval in form, with a well-developed peristome sinistrally twisted. There is frequently a large pigmented spot at the anterior end of the body. 0·3. Marine and freshwater. *Spirostomum*, Ehrb. The longest of all the Ciliata. It contracts rapidly in a spiral manner. Very large elongated contractile vacuole. Numerous micronuclei. 3 mm. in length when fully extended. Marine and freshwater. (Figs. 57, 58.)

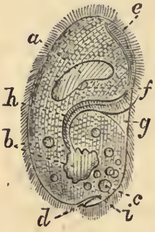

FIG. 56.

*Nyctotherus cordiformis*, Ehrb., as seen from the right side. *a*, meganucleus; *b*, a water vacuole; *c*, contractile vacuole; *d*, anus; *e*, band of long cilia; *f*, micronucleus; *g*, mouth; *h*, pharynx; *i*, short cilia. (After Stein.) Size about ·15 mm. in length.

Family BURSARINA, Bütschli. *Thylakidium*, Schew. With a long ventral peristome. The medulla contains numerous zoochlorellae. Freshwater in Australia. *Balantidium*, Clap. and L. A large peristome and well-marked anal aperture. 0·5. Very common in the rectum of Batrachia, occasionally found in the large intestine of man and in the coelom of Annelida. *Balantidiopsis*, Bütschli. A smaller peristome than in *Balantidium*. 0·15. Intestine of Rana esculenta. *Condylostoma*, Duj. Club-shaped in form. The right border of the peristome bears a large undulating lip. 0·5. Marine and freshwater. *Bursaria*, Clap. and L. The peristome is an enormous excavation on the anterior and ventral face of the body. Meganucleus strap-shaped. Micronuclei 16 or more. 1·5. Very common in some freshwater ponds. (Figs. 58 and 59.) *Bursaridium*, Lauterb.

Family STENTORINA, Stein. *Climacostomum*, Stein. The form of the body is oval and shows little contractility. The peristome is large and oblique. It is in many ways intermediate between *Balantidium* and the STENTORINA. 0·36. Freshwater. *Stentor*, Oken. Elongated trumpet-shaped form, with a well-developed adoral zone at the broadest end. A long moniliform meganucleus and several

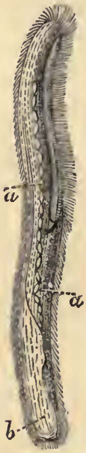

FIG. 57.

*Spirostomum ambiguum*, Ehrb. On the right side of the peristome the long cilia of the adoral zone. *a*, *a*, moniliform meganucleus; *b* points to the enlarged part of the contractile vacuole; in front of this letter it is drawn out into a narrow tube. × 100.

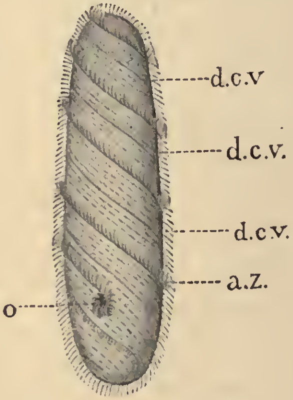

FIG. 58.

Spirally contracted condition of *Spirostomum ambiguum*, Ehrb. *d.c.v*, the duct of the contractile vacuole; *a.z*, adoral zone; *o*, mouth. (From Bütschli, after Lieberkühn.) × 120.

micronuclei. Some species coloured blue with Stentorin, others red, brown, green, or colourless. They swim rapidly with a rotatory movement, or attach themselves by their narrow posterior ends to a foreign object. Sometimes, in the sedentary condition, they form gelatinous tubes. 1 mm. or more in length when fully extended. Freshwater. (Fig. 61.) *Folliculina*, Lamark. The peristome extended into a pair of large, lateral, wing-like processes. It

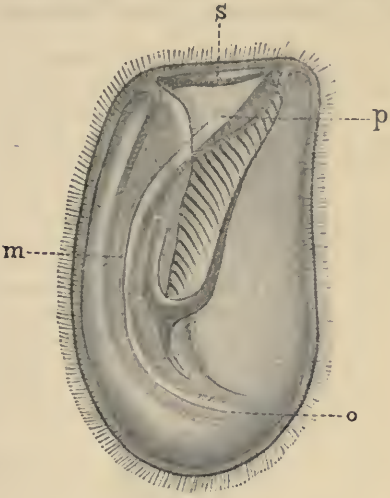

Fig. 59.

*Bursaria truncatella*, O.F.M. The peristome is, in this form, a deep excavation, the margins of which embrace a considerable part of the anterior and ventral surfaces (*p*). It can be closed by a sphincter myophan band (*s*). A thin vertical fold projects into this cavity on the right side (left in the figure), and a thicker striated fold projects into it on the left side. On the dorsal side there is a gutter (*m*) leading down to the mouth, and this is continued into a narrow oesophagus (*o*). (After Schuberg.) × ca. 50.

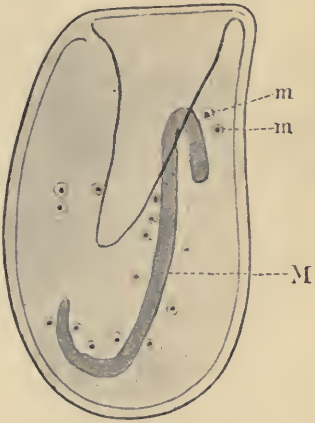

Fig. 60.

*Bursaria truncatella*, O.F.M. Diagram of a preserved specimen to show the long strap-shaped meganucleus (*M*), and 16 micronuclei (*m*, *m*). (Constructed from the researches of Prowazek.)

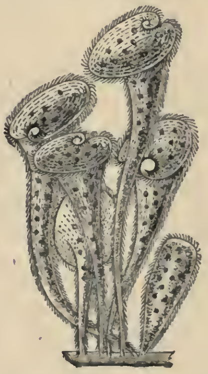

Fig. 61.

*Stentor polymorphus*, Müller. A group of individuals attached to a water weed. × 50.

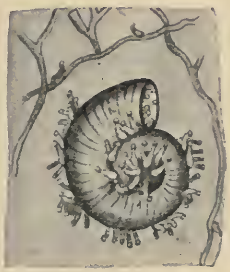

Fig. 62.

An empty Spirorbis shell bearing a large number of the tests of *Folliculina ampulla*. (After Stein.) × ca. 5 diam.

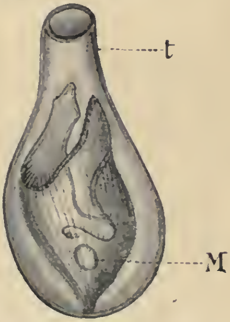

Fig. 62a.

A specimen of *Folliculina* as it is seen when retracted into its test (*t*). (After Stein.)

is extremely contractile. It forms chitinous tubes attached to Algae and Shells. 1 mm. when fully extended. Marine and sometimes freshwater. (Figs. 62, 62A, 63.)

Family Gyrocoryna, Stein. *Caenomorpha*, Perty. The remarkable form of this genus is shown in Fig. 64. Its general relations seem to be with *Metopus*, one of the Plagiotomina. On the other hand, the absence of cilia from all but localised parts of the body indicates affinities with the Oligotricha. 0·1. Freshwater and marine. Closely allied to it is *Caenomorphina*, Blochmann.

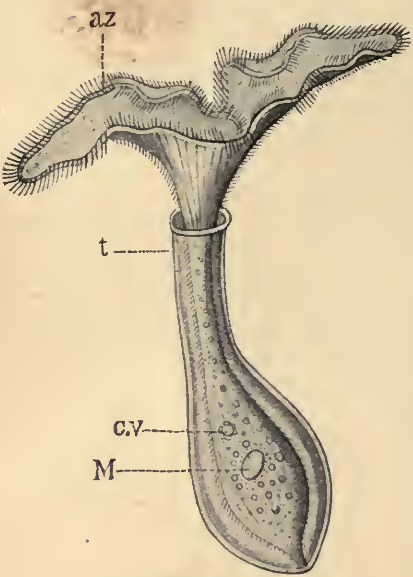

Fig. 63.

*Folliculina ampulla*, C. and L., expanded. *a.z*, the bilobed adoral zone; *t*, the test; *c.v*, contractile vacuole; *M*, meganucleus. (After Stein.) × ca. 150.

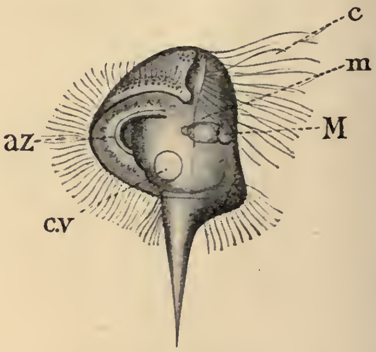

Fig. 64.

*Caenomorpha medusula*, Perty. From the ventral side, slightly turned to the right. *a.z*, adoral zone; *c.v*, contractile vacuole; *M*, meganucleus; *m*, micronucleus; *c*, cirri. (From Bütschli, after Blochmann.) × 300.

## Sub-order Oligotricha.

In this group the adoral zone is always situated at the free or anterior extremity of the body. In nearly all forms there are areas or tracts of the surface of the body free from cilia, and in a considerable number of genera there are localised tufts of cilia (*Cycloposthium*) or spinous processes of the body-wall (*Ophryoscolex*). The body is very variable in shape, and no particular form of it can be regarded as characteristic of the sub-order. The sub-order includes a large number of species (Tintinnoina, etc.) of small size which occur in the plankton of the sea and lakes. These animals very frequently exhibit curious and very characteristic darting movements alternating with periods of immobility. Several genera are internal parasites. The meganucleus is usually a single large oval body, and is accompanied by one micronucleus.

The Oligotricha are divided into the following families:—

Family Lieberkühnina (?), Bütschli. Bütschli founded this family to include certain spherical forms with a spiral adoral zone which were regarded by Claparède and Lachmann and Lieberkühn as young stages of *Stentor*. Freshwater.

Family Halterina, Cl. and L. *Strombidium*, Cl. and L. More or less conical in shape, with a spiral adoral zone of long and strong cilia. There are in addition a few cilia on the ventral surface. 0·04. Marine and freshwater. (Fig. 65.) *Torquatella*, Lankester. Closely related to *Strombidium*, but with adoral cilia united to form a membranous collar. A supra-oral papilla. (Figs. 12 and 66.) Found associated with the eggs of Terebella. *Halteria*, Duj. Spherical in form, with tactile processes scattered on the posterior hemisphere of the body. It remains motionless for some time and then suddenly darts forward to another position, where it again assumes its immobility. 0·04. Freshwater.

Family Tintinnoina, Clap. and L. These are minute forms which build a gelatinous or chitinous protective shell or case. *Tintinnidium*, Saville Kent. The case is gelatinous and tubular, sometimes free, sometimes attached to foreign objects. Freshwater. *Tintinnus*, Fol. With a chitinous shell shaped like a test-tube with a slightly constricted neck. 0·3. Marine. *Tintinnopsis*, Stein. Shell conical in shape, very thin, and sometimes strengthened by agglutinated foreign particles. 0·2. Pelagic plankton. *Codonella*, Haeckel. Pot-shaped shell, ornamented with hexagonal ridges. (Figs. 67 and 68.) In some species there is an apparatus for closing the orifice of the shell. 0·1. Marine and freshwater. *Ptychocylis*, Brandt. Marine. *Porella*, Cleve. Marine. *Dictyocysta*, Ehrb. 0·1. Marine.

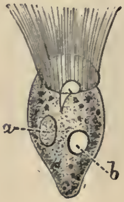

Fig. 65.

*Strombidium claparedii*, Kent. *a*, meganucleus; *b*, contractile vacuole. × 200.

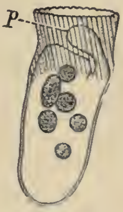

Fig. 66.

*Torquatella typica*, Lankester. Side view to show the supra-oral papilla (*p*) as seen through the membranous collar. Cf. Fig. 12.

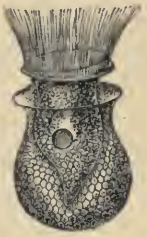

Fig. 67.

*Codonella lagenula*, Cl. and L. × 200.

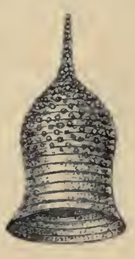

Fig. 68.

Empty shell of *Codonella campanella*, Haeckel. × 180.

Family Ophryoscolecina, Stein. The following genera composing this family occur in the rumen of the cow and some other Artiodactyla. *Ophryoscolex*, Stein. At the anterior extremity there is a funnel-shaped peristome provided with many large cilia. Running spirally round the anterior end of the body there is an adoral membranella provided with a few thick cilia. There is a well-marked anus. At the posterior end of the body there is a spinous prolongation of the cortex, and similar spinous processes occur in circular elevations for some considerable distance in front of it. There are several contractile vacuoles. 0·1-0·3. *Entodinium*, Stein. Oval in form, with a spinous caudal process. No spiral membranella round the body. 0·03-0·12. *Diplodinium*, Schuberg, differs from *Entodinium* in the presence of a portion of the adoral membranella on the left side of the body. The genera *Cycloposthium*, Bundle (Fig. 69), and *Didesmis*, Fior., from the coecum of the horse, should be separated into a distinct family.

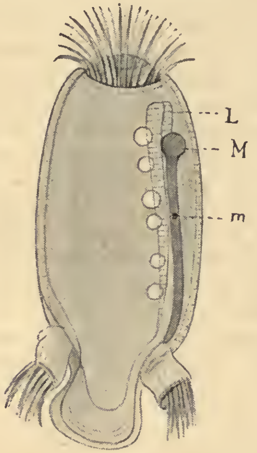

Fig. 69.

*Cycloposthium bipalmatum*, from the coecum of the horse. *M*, meganucleus; *m*, micronucleus; *L*, peculiar vacuolated band by the side of which is situated a row of contractile vacuoles. (After Günther.)

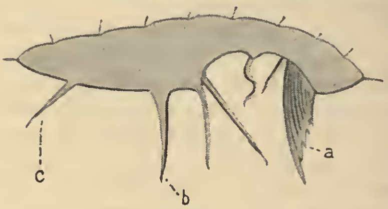

Fig. 70.

Diagrammatic transverse section through the body of a Hypotrichous Ciliate in the region of the peristome. *a*, membrane overhanging the mouth; *b*, a ventral cirrus; *c*, a lateral cirrus. On the dorsal side are rows of stiff, bristle-like cilia. (After Sterki.)

Appendix.—The genus *Maryna*, Gruber, is probably related to the Tintinnoina, and should be included in the Oligotricha. The individuals live in colonies which form a system of dichotomously branched mucous tubes. Freshwater.

## Order **Hypotricha**, Stein.

The genera included in this order are usually characterised by a well-marked compression of the body in the dorso-ventral axis. The dorsal surface has no movable cilia, but is usually provided with a few scattered, stiff, bristle-like processes of the pellicle (Fig. 70). The ventral surface is provided with a continuous covering of short cilia, arranged in longitudinal rows, in the more primitive forms (*Urostyla*, *Peritromus*), or with more differentiated rows or groups of cirri and membranellae associated or not with small cilia. The most important of the cirri are usually arranged in three groups (cf. Fig. 1), one just behind the anterior margin called the frontal cirri, a row usually running transversely across the posterior ventral surface called the caudal cirri, and between these two groups a number of abdominal cirri (3-10) arranged

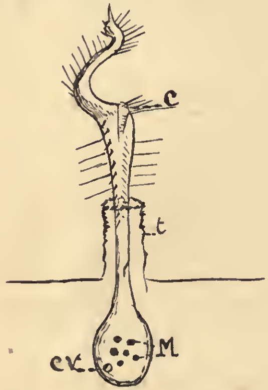

Fig. 71.

*Stichospira paradoxa*, Sterki. Length about ·04 mm. Living in a cavity of a leaf which is extended forward by the addition of a tube (*t*) built by the animal itself. *c*, mouth; *M*, meganuclei; *c.v*, contractile vacuole. (After Sterki.)

in irregular rows or unevenly scattered. The HYPOTRICHA are usually found creeping on the surface of animals, plants, the scum of putrefactions, or the surface film of water. The progression is effected entirely by the cilia or cirri on the ventral surface of the body, which are used like the legs of higher animals. The most modified form is *Stichospira* (Fig. 71), which is elongated in shape and uses its ventral cirri to crawl up and down a short mucilaginous tube which it constructs on the epidermis of plants.

The HYPOTRICHA are nearly all small (·3 to ·4 mm.) or very small (·03-·01 mm.) in size, and they are usually very active in their movements. The meganucleus sometimes exhibits a remarkable fragmentation during the intervals between the acts of fission as described on p. 372 (Figs. 16 and 17). A majority of the genera have been described by authors as possessing either two nuclei or a single two-jointed nucleus. It is probable that this double- or twin-nucleus condition is one phase, characterised by its considerable duration, in the process of nuclear fragmentation. *Stylonychia* and *Euplotes* each possess one minute micronucleus, but in most of the genera very little is known about the micronuclei.

The order HYPOTRICHA is divided into the following families:—

Family PERITROMINA, Stein. *Peritromus*, Stein. This is the simplest form of the HYPOTRICHA, the ventral ciliation being uniform and dense and without any differentiation of stouter cilia or cirri. 0·1. Marine.

Family OXYTRICHINA, Stein. *Trichogaster*, Sterki. 0·23. Freshwater. *Urostyla*, Ehrb. Elongated in form. Ventral cirri arranged in five or more longitudinal rows. Enlarged cirri in the frontal region and in a transverse row near the posterior extremity. 0·3. Marine and freshwater. *Kerona*, Ehrb. Kidney-shaped. Six or seven oblique rows of small cirri on the ventral side. 0·15. Found creeping on the ectoderm of Hydra. *Epiclintes*, Stein. The number of rows of ventral cirri is reduced to five or six, but there are no special frontal or caudal cirri. 0·3. Marine. *Stichotricha*, Perty. The anterior extremity is prolonged into an extremely flexible proboscis, on which the adoral zone is extended. Either free or attached by gelatinous tubes, which sometimes form dendritic colonies. 0·1. Marine and freshwater. *Stichospira*, Sterki. On freshwater plants (Fig. 71). *Strongylidium*, Sterki. Freshwater. *Holosticha*, Entz. Two rows of marginal cirri, between which are two or three rows of cirri without special differentiation of frontal cirri. A tranverse row of caudal cirri. 0·4. Marine. *Amphisia*, Sterki. With differentiated frontal cirri. Marine and freshwater. *Uroleptus*, Ehrb. Three well-developed frontal cirri. Sometimes rose or violet in colour. 0·5. Marine and freshwater. *Sparotricha*, Entz. Similar to *Spirotricha*, but the adoral zone does not extend beyond the middle of the proboscis. 0·1. Salt marshes in Hungary.

Family PLEUROTRICHINA, Bütschli. In this family the frontal cirri are well developed and usually eight in number. There are also specialised abdominal and caudal cirri. *Onychodromus*, Stein. Three or four abdominal cirri. 0·35. Freshwater. *Pleurotricha*, Stein. Five strongly-developed abdominal cirri and a row of five transverse caudal cirri. 0·4.

Freshwater. *Gastrostyla,* Engelmann. A row of several well-developed ventral cirri. 0·32. Freshwater. *Gonostomum,* Sterki. Very small peristome. 0·20. Marine and freshwater. *Urosoma,* Kowalewsky. Posterior end drawn out into a long caudal process. Eight abdominal cirri. 0·24. Freshwater. *Oxytricha,* Ehrb. Five abdominal and five caudal cirri. Caudal spines usually present, but not well developed. 0·2. Freshwater and marine. *Stylonychia,* Ehrb. The right margin of the peristome is bent in an S-shaped curve. Three very long caudal spines (Figs. 72 and 73). 0·4. Fresh water and marine. *Histrio,* Sterki. Closely related to *Stylonychia.* Freshwater. *Actinotricha,* Cohn. Peristome reduced in size. The left border bears a number of large membranellae arranged in the form of a fan. 0·1. Marine.

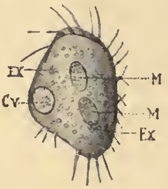

FIG. 72.

*Stylonychia pustulata* previous to encystment. The granules of waste matter (*Ex*) collected in clusters, some of them already discharged; *M, M,* meganuclei; *c.v,* contractile vacuole. (After Prowazek.)

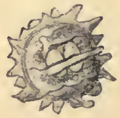

FIG. 73.

Cyst of *Stylonychia pustulata.* (After Prowazek.)

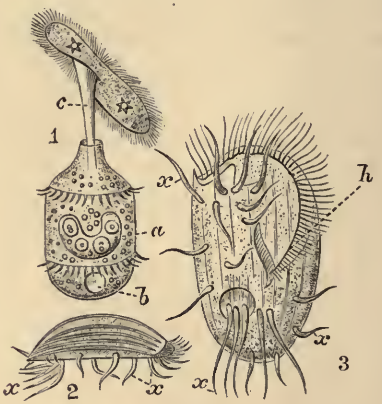

FIG. 74.

1, *Didinium nasutum,* Müller, one of the GYMNOSTOMATA, see p. 399. × 200. The pharynx is everted and has seized a *Paramoecium* as prey. 2, *Euplotes charon,* Müller. Side view. A tuft of frontal cirri may be seen in front (right of diagram); a few abdominal (*x*) in the middle of the ventral side; and a group of five (*x*) forming the transverse row of caudal cirri. 3, *Euplotes harpa,* Stein. × 150. Ventral view. *h,* mouth; *x,* hypotrichous processes.

Family PSILOTRICHINA, Bütschli. Small forms in which the frontal and abdominal cirri are not clearly differentiated. *Balladina,* Kow. All the cirri are remarkably elongated. 0·04. Freshwater. *Psilotricha,* Stein. Anterior end broad, posterior end more constricted. Very broad peristome. 0·1. Freshwater. *Dipleurostyla,* Roux. Freshwater.

Family EUPLOTINAE, Stein. The principal character is the great reduction in the ciliation of the body. *Euplotes,* Stein. (Fig. 74, 2.) Peristome extensive. Six or seven frontal cirri and a transverse band of five cirri in the caudal region. 0·2. Freshwater and Marine. *Diophrys,* Duj. The peristome even more extensive than in *Euplotes,* reaching as far back as the row of caudal cirri. 0·15. Marine. *Uronychia,* Stein. The frontal cirri missing. 0·1. Marine.

Family Aspidiscina, Stein. *Aspidisca*, Ehrb. The peristome is entirely on the left side. Marginal cirri completely reduced. Meganucleus band-shaped. 0·07. Marine and freshwater.

### Order **Peritricha**, Stein.

In this order the cilia are generally confined to a single spiral girdle situated at the margin of the adoral disc, and the vestibule. In *Trichodina*, *Cyclochaeta*, and *Licnophora* there is a second girdle of cilia at the aboral end. In some cases the adoral girdle of cilia is surrounded by a ridge or collar of the pellicle which is not ciliated, and in some species of *Vorticella*, etc., this can be constricted above the adoral disc during retraction in a similar manner to the constriction of the margin of the disc of a sea-anemone. In *Spirochona* there is a delicate spiral membrane at the adoral end of the body (Figs. 22 and 23), but it is difficult to determine whether this membrane should be regarded as due to a fusion of the cilia of a spiral girdle or to an exaggeration of a spiral collar. The general surface of the body of the Peritricha is naked. Nearly all the Peritricha are sedentary in habit during the greater part of their existence. The Licnophorina readily leave their host and swim away. Many of the Vorticellina break away from their peduncles and form a new one when another suitable situation for attachment is found. The tubicolous forms leave their shelter if the food supply fails and seek another locality. It is probable, indeed, that none of the Peritricha are absolutely sedentary.

In the more primitive forms the attachment is made by the aboral disc, which acts like a sucker and can readily be released. The disc may be provided not only with a peripheral girdle of cilia, but also with an armament of hooks (*Trichodina*) or cirri (*Cyclochaeta*).

In *Spirochona* and *Kentrochona* (Figs. 3 and 22) the adhesive disc is a simple expansion of the body-wall, sometimes exhibiting pseudopodial lobes.

The arrangement of the spiral girdle or collar may be either left-handed (scaiotrichous) as in the Licnophorina and Spirochonina, or right-handed (dexiotrichous) as in the other Peritricha with a spiral girdle.

In *Epistylis* and *Opercularia* the body is provided with a long rigid stalk or peduncle, and in *Carchesium* and *Vorticella* with a peduncle that is capable of very rapid spiral contraction. The genera *Cothurnia* (Fig. 81), *Vaginicola*, etc., secrete a shell or tube which is attached to some animal or plant, and in *Ophrydium* a colony of stalked individuals (Fig. 2) secretes a common mucilaginous investment.

The Peritricha may be either solitary in habit (*Vorticella*, *Spirochona*, *Cothurnia*) or associated together in colonies (*Epistylis*, Fig. 78, *Carchesium*, *Ophrydium*, Fig. 2).

The mouth is usually situated at the bottom of a deep, ciliated, funnel-shaped vestibule (see Fig. 27), and may open into a globular pharyngeal vacuole. The anus (cytopyge) usually opens near the mouth of the vestibule (Fig. 27), but is, with rare exceptions, only temporarily open. In *Epistylis umbellaria* large nematocysts occur (Fig. 75), but these organs are absent in other Peritricha.

The meganucleus of the Peritricha is usually a long, bent, horse-shoe-shaped, or strap-shaped body. The micronucleus is, in the resting condition, extremely minute and difficult to observe. Only one micronucleus is usually present in each individual.

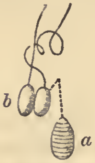

FIG. 75.

Nematocysts of *Epistylis umbellaria*. *a*, with the thread at rest; *b*, with the thread discharged. (After Greef.) Each capsule is about 85 μ in length.

The order PERITRICHA is divided into the following families:—

Family SPIROCHONINA, Stein. *Spirochona*, Stein. (Fig. 22.) Attached to the gills of Gammarus by a sucker. Mouth surrounded by a delicate spiral membrane, the inner surface of which is partially provided with extremely minute cilia. Reproduction by external gemmation. Meganucleus oval or spherical, with a clear zone containing in the resting state a single chromatin body—the nucleolus (?). One to three micronuclei. 0·12. Gills of Gammarus. *Kentrochona*, Rompel (Fig. 3). Adoral membrane in the form of a large wide-mouthed funnel, not spirally twisted. This is supported by four columnar thickenings which project as spines from the margin of the funnel. Meganucleus spherical. 3-4 micronuclei. 0·04. On the limbs of Nebalia. *Kentrochonopsis*, Doflein. With multiple endogenous gemmation. Six micronuclei. Gills of Nebalia geoffroyi. *Chilodocona*, Wallengren. Maxillae and maxillipedes of Ebalia and Portunus.

Family LICNOPHORINA, Bütschli. Spiral girdle scaiotrichous and ciliated. *Licnophora*, Clap. Aboral sucker surrounded by a circle of cilia. 0·12. Attached to several marine Invertebrata such as Medusae, Pelecypoda, Polychaeta, etc.

Family VORTICELLINA, Bütschli. *Trichodina*, Stein. Cylindrical in form, with an adhesive disc surrounded by a ring of cilia. 0·1. Found on the surface of Hydra, Sponges, Planarians, and other freshwater animals; and also occasionally in the bladder of Frogs, Newts, and Fishes. *Cyclochaeta*, Jackson. With a ring of very long bristle-like processes just above the ring of cilia of the adhesive disc. 0·1. On Spongilla, on the gills of Scorpaena, Trigla, and Serpula, and on the surface of Asteriscus and Ophiothrix. *Trichodinopsis*, Clap. and L. A remarkable form, with a very much constricted oral extremity, causing the body to assume a conical shape. The whole surface of the body between the oral and aboral rings of cilia covered with long cilia. 0·13. Parasitic in the gut and lung of Cyclostoma. *Scyphidia*, Lachmann. Cylindrical forms without a stalk and without an aboral ring of cilia. 0·12. Attached by the aboral sucker to the skin of freshwater and marine Mollusca. *Gerda*, Clap. and L. Cylindrical in form, with the oral region considerably constricted. Very contractile. When swimming, a ring of cilia is formed at the aboral end. 0·2. Freshwater. *Hastatella*, Erlanger. With long spinous processes. Stagnant freshwater. *Astylozoon*, Engelmann. Free, with a pointed posterior extremity provided with two or three saltatory bristles. 0·1. Freshwater. *Vorticella*, Linnaeus, 1767, emend. Ehrb., 1838. (Figs. 76 and 77.) This genus is now confined to those Vorticellids with a simple unbranched contractile stalk. A large number of species have been described, but as there is great

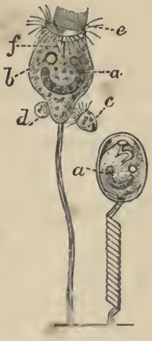

FIG. 76.

*Vorticella microstoma*, Ehrb. On the left a female with two males (*c.d*) attached to it. Only one (*d*) is in the act of conjugation. *a*, meganucleus; *b*, contractile vacuole; *e*, ciliated disc; *f*, vestibule. On the right an individual with the stalk contracted and the body enclosed in a cyst.

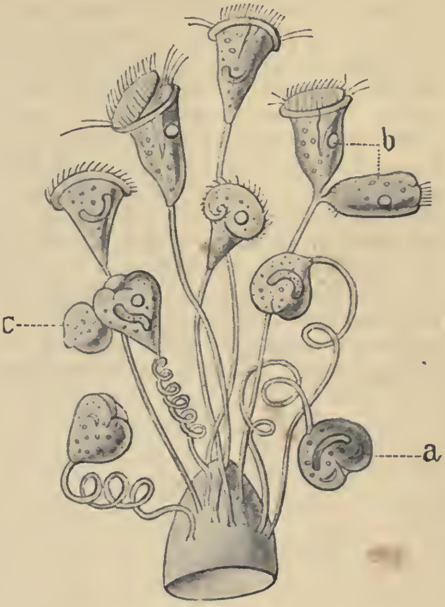

FIG. 77.

*Vorticella nebulifera*, Ehrb. A social group showing at *a* and *b* successive stages of fission, and at *c*, conjugation. (After Saville Kent.)

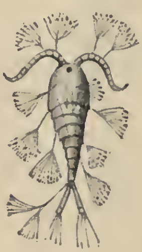

FIG. 78.

Cyclops with several colonies of *Epistylis anastatica* attached to the antennae and somites. (After Saville Kent.) × 10.

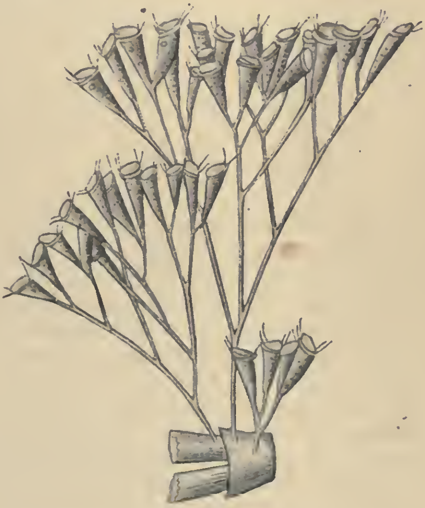

FIG. 79.

*Epistylis anastatica*, Linn. Colonial stocks attached to the limbs of Cyclops. (After Saville Kent.) × 100.

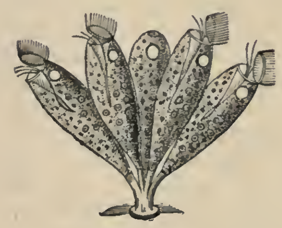

FIG. 80.

*Opercularia stenostoma*, Stein. Observe the undulating membrane of the oral vestibule and the oblique ciliate disc. × 200.

difficulty in distinguishing between true specific characters and local variations, a great many of the described species are not generally recognised as distinct. 0·2 in height. Cosmopolitan in freshwater, also marine. *Carchesium*, Ehrb. With contractile, branched, and colonial stalks. The colonies sometimes 4 mm. in height. Attached to freshwater plants and animals in Europe and N. America. *Zoothamnium*, Ehrb. In Carchesium every new individual that is formed secretes its own peduncle, and retains its power of independent contraction. In *Zoothamnium*, on the contrary, the peduncle of the parent splits during fission as far down as the next branch, and the colony retracts as a whole. Individuals 0·08. Colonies sometimes several mm. in length. Marine and freshwater. *Glossatella*, Bütschli. Stalk very rudimentary. An enormous undulating membrane round the peristomial margin. 0·04. Attached to Triton larvae. *Epistylis*, Ehrb. Forming colonies similar to those of *Carchesium*, but with non-contractile peduncles. (Figs. 78 and 79.) Colonies 4 mm. in height. Individuals 0·8. Principally found attached to freshwater animals. (Figs. 78 and 79.) *Rhabdostyla*, Kent. Similar to *Epistylis*, but solitary. ·09. On larvae of Diptera. *Opercularia*, Stein. (Fig. 80.) The disc is oblique, and the peristome is provided with an undulating membrane. Peduncle as in *Epistylis*, branched and rigid. 0·25. Freshwater. *Campanella*, Goldfuss. The adoral zone of cilia greatly developed, forming five complete turns. 0·15. Colony 4 mm. Freshwater. *Ophrydium*, Ehrb. (Fig. 2.) Colony secreting a common mucilaginous test. 0·4. Freshwater. *Cothurnia*, Clap. and L. Individuals secrete a cylindrical test, provided with a lid which can shut down over the contracted individual. (Figs. 81, 82, 83.) 0·4. Marine and freshwater. *Cothurniopsis*, Entz. Individuals usually more isolated than in Cothurnia. Commonly found on the gills of Astacus

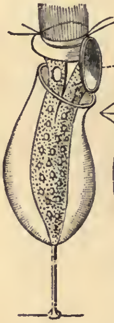

Fig. 81.

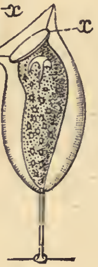

Fig. 82.

81. — *Cothurnia* (Pyxicola, Kent) *affinis*, Kent. Expanded. *x*, operculum.

82. — *Cothurnia* (Pyxicola, Kent) *affinis*, Kent. Retracted. *x*, operculum closed.

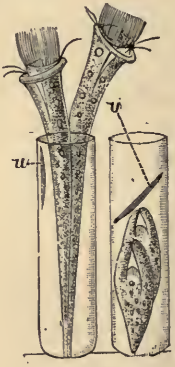

Fig. 83.

*Cothurnia* (Thuricola) *valvata*, Wright. On the left two expanded individuals are, as a result of fission, temporarily occupying one tube. *u*, valve. On the right, the same retracted, the valve *u* closed like the door of a trap-door spider's nest.

and other freshwater Crustacea. Probably also marine. *Vaginicola*, Clap. and L. Test of the shape of a recumbent soda-water bottle. 0·1. Attached to freshwater plants. *Lagenophrys*, Stein. Forming a spherical mucilaginous test. 0·07. Attached to the gills of Gammarus and Asellus. *Nematopoda*, Sand.

### APPENDIX TO THE CILIATA.

Family TRICHONYMPHIDAE, Leidy. It is a matter of considerable difficulty, with our present knowledge, to determine the exact relations of this family. The long cilia, some mobile and some immobile, the general shape of the body, and the endo-parasitic habit, suggest relations with some of the endo-parasitic Holotricha. On the other hand, the absence of a definite mouth, associated with the habit of engulphing solid food at indefinite parts of the general surface of the body, is a condition which definitely separates them from any of the orders of the Ciliata. Micronuclei have not yet been described, and it is therefore possible that they are homokaryote.

The TRICHONYMPHIDAE occur in immense numbers in the intestines of certain Orthoptera, more particularly in Termes flavipes. In *Trichonympha* (Fig. 11) the body is differentiated into three regions—an anterior translucent knob, a middle or bell-shaped part, and a posterior part or body. The anterior knob is extremely active in the living animal, and constantly in motion. The shorter cilia of the middle region are active, and produce the movements of the body. The longer cilia of the posterior part are absolutely motionless, and are said to entangle particles which become subsequently engulphed by the protoplasm of this region (Porter). In *Pyrsonympha* the anterior knob is prolonged into a very delicate filament, which perforates the epithelium of the intestine of the host and serves as a means of attachment. The ciliation of the body is, in this fixed form, very much reduced.

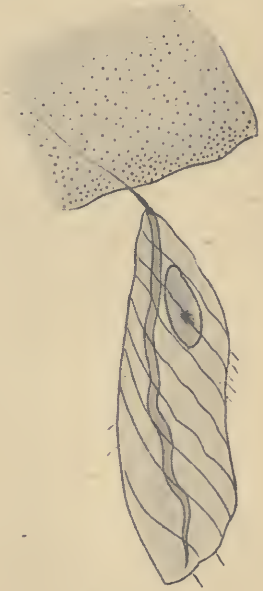

FIG. 84.

*Pyrsonympha vertens*, Leidy, attached by a delicate filament to the epithelium of the intestine of Termes flavipes. The filament appears to be continuous with a specialised (muscular?) band running through the whole length of the medulla. (After Porter.) × 400.

The genera of TRICHONYMPHIDAE are: *Lophomonas*, Stein. The flagellate cilia are confined to a horse-shoe-shaped crescent at the anterior end of the body. 0·03. Rectum of Periplaneta, Gryllotalpa. *Leidyonella*, Frenzel. Anterior extremity prolonged to form a short neck, in other respects similar to Lophomonas. 0·45. Rectum of Eutermes. *Trichonympha*, Leidy. Body divided into three regions, all provided with long flagellate cilia. 0·12. Rectum of Termes. *Joenia*, Grassi. Similar to Lophomonas, but more elongated, and with a number of short non-mobile cilia at the posterior end. Rectum of Callotermes. *Pyrsonympha*, Leidy. (Fig. 84.) With a long anterior flagellum of attachment. 0·1. Rectum of Termes. *Dinennympha*, Leidy. More elongated than Pyrsonympha, and spirally twisted. 0·1. Rectum of Termes.

## CLASS ACINETARIA, Lankester

The majority of the animals included in this class are permanently or temporarily sedentary in habit. It seems probable, however, that some of the species of the genus *Sphaerophrya* may be permanently free.

The characteristic feature of the class is the possession of the organs known as Suckers, Tentacles, and Arms. The morphology of these organs is discussed in another place (p. 370).

In *Rhynceta* (Fig. 13) there is only one sucker, and in *Hypocoma*, which may be only a persistent larval form, the single ventral sucker is supplemented by a patch of cilia on the same aspect of the body. In *Sphaerophrya* the body is furnished with a few suckers evenly distributed, and in the pedunculate *Acineta* there are numerous suckers scattered on the surface that is free. In some species of *Ephelota* the suckers and tentacles are evenly distributed on the free surface, whilst in *Tokophrya*, *Podophrya*, and *Solenophrya* the suckers are restricted to three or four bunches at the angles of the disc. In *Dendrocometes* these bunches of suckers are represented by 4-6 arm-like processes of the body-wall, and very probably the 1-4 arms of the remarkable genus *Ophryodendron* have a similar significance.

The attachment of the individual to the host or to some foreign weed or other substance may be effected by a broad flattened base as in *Dendrocometes*, *Dendrosoma*, *Solenophrya*, or by a stiff cuticular peduncle with a protoplasmic core as in *Acineta* and *Podophrya*.

There is, as a general rule, no mouth, the food being held by one or more of the suckers and the dissolved products passing down the suckers into the general protoplasm of the body.

The body-wall is covered with a thin pellicle which is in many forms finely loricate. Some species have the power of withdrawing themselves from this pellicle, which is left behind as a shell, together with a certain amount of cytoplasm. They then develop a temporary covering of cilia and swim away to a more suitable locality. The cilia disappear when the individual again becomes fixed. This has been observed in *Dendrocometes*, but it probably occurs in other genera as well (*Podophrya* and *Metacineta*).

The peduncle of the Acinetaria appears to be formed as a secretion by the pellicle of the inferior surface of the body, and it is never contractile. In many forms it expands distally to form a saucer-shaped expansion (*Podophrya*, *Ephelota*) for the support of the body or (*Metacineta*) a protective cup for its reception during retraction.

A large number of the Acinetaria are epizoic in habit, and very frequently a particular species is only found on one genus of host. For example, *Rhynceta* occurs only on the abdominal appendages of Cyclops, and *Dendrocometes* on the gills of Gammarus. The species of *Ephelota* are frequently associated with particular species of Hydroids; *Stylocometes* is usually found on the gills of Asellus, but has also been found on the colonies of Ophrydium. The species of *Acineta* are usually found attached to water weeds. Some species of *Sphaerophrya* after a brief free-swimming life in the water attack various Ciliata and become parasitic. *Endosphaera* is parasitic on *Vorticellina* and some Acinetaria. The phenomenon of conjugation has been observed in *Dendrocometes*, *Podophrya*, *Tokophrya*, and probably occurs throughout the group. In *Podophrya* the discs of two neighbouring individuals are brought together and fusion of the protoplasm of the two is thus effected. In *Dendrocometes* and *Stylocometes*, however, a special pseudopodium from the body-wall of each of two neighbouring individuals is produced, and these meet and fusion takes place. It would be interesting to know what stimulus causes these processes to form at the same time and grow together. The reproduction is usually brought about by gemmation. In the parasitic species of *Sphaerophrya* a division into two equal halves takes place soon after the parasites have reached their full size. This is followed by a rapid series of equal divisions, and finally the spores that are thus formed develop suckers and escape as small free-floating individuals. At this stage a division occurs into two almost equal segments, but the smaller of the two is provided with suckers and cilia, and may be regarded as a bud, while the larger, which has suckers but no cilia, may be regarded as a parent. There is, however, no sharp line to be drawn between the processes of fission and gemmation in these animals: they are probably of essentially the same nature. But the case of *Sphaerophrya* is interesting as it exhibits two phases of the reproductive processes (fission in the parasitic form, gemmation in the free) which are very closely related, but sufficiently distinct to justify a different nomenclature.

In the stalked forms *Podophrya* and *Metacineta*, the disc divides horizontally into two almost equal parts, but the distal part is ciliated and has no suckers, whilst the proximal part attached to the stalk has suckers and no cilia. In *Dendrocometes* there is a division into two approximately equal parts, but in this case the smaller ciliated part or bud is separated from the other internally and remains for a little while free inside a chamber (brood chamber) of the other part or parent, which is provided with arms and is not ciliated. The application of the terms "gemmula" and "parent" to the two parts in this case is clearly appropriate.

In many species of *Ephelota* a number (6-16) of gemmulae are formed at the free surface of the disc, and these may be ciliated (Fig. 14), or provided with tentacles and a small special disc of cilia (Fig. 96), when they are set free. Finally, in some species of *Acineta* and in *Ophryodendron*, several ciliated buds are formed in a chamber similar to the chamber containing the single bud in *Dendrocometes.*

The free-swimming buds of the Acinetaria are frequently called the "embryos," but as this term may lead to a misunderstanding as to their origin, it is better to call them simply buds or "gemmulae." The gemmulae are sometimes oval in shape, as in certain species of *Sphaerophrya*, *Podophrya* (Fig. 20), *Ephelota*, etc.; spherical, as in certain species of *Trichophrya;* or plano-convex, as in *Dendrocometes.* As regards the ciliation, they may be holotrichous, as in *Tokophrya elongata;* or hypotrichous, as in *Hypocoma*, *Ephelota gemmipara*, etc. The form of ciliation which is most commonly met with is that of a broad band or girdle encircling the equator of the gemmula, or two or more narrow bands arranged in a peritrichous manner as in *Dendrocometes* and *Dendrosoma* (Figs. 86 and 33).

The method of feeding of the Acinetaria is remarkable. The suckers have the power of seizing and holding fast Ciliate and other Protozoa of considerable size. This power might be explained on the supposition that they can exert a sucking action, but there can be no doubt that the prey is not only held fast but also stunned or paralysed in some way by the Acinetarian. Very soon after the prey is secured very small globules may be seen passing rapidly down the sucker (or arm) into the cytoplasm of the disc, proving that the paralysis of the prey is quickly followed by the digestion of its protoplasm and its absorption in a liquid form.

Very little is known about the encystment of the Acinetaria. Some species of *Podophrya* and *Ephelota* form cysts which are probably more resistant to unfavourable physical conditions than the active phase of life. *Dendrocometes*, however, and probably other genera, may be found at all times of the year, and never show any signs of encystment.

There is considerable difficulty in dividing the Acinetaria into families, as the whole life-history of very few species has yet been worked out. Sand has shown that *Podophrya gelatinosa*, Buck, passes from the ciliated gemmula into a stage similar to *Sphaerophrya*, and that from the *Sphaerophrya* stage it changes into a form like *Trichophrya* before it assumes the adult *Podophrya* form. In this stage it may separate from the peduncle, become ciliated again, and then change into a *Sphaerophrya* and reproduce by fission or develop a new stalk and return to the *Podophrya* condition. If other species have a similar life-history, as is very probable, our classification must be regarded as quite provisional.

The Acinetaria contain the following families according to the classification of Sand:—

Family Dendrocometina, Stein. Epizoic Acinetaria of medium size without a peduncle. Hemispherical or lenticular in shape. Numerous tentacles arranged in several bundles, the individual tentacles being fused together for the greater part of their course to form the "arms," but independent at their free extremities. Each contains a single contractile vacuole. Reproduction by the formation of a single endogenous gemmula. *Dendrocometes*, Stein, is found on the gills of Gammarus pulex. In Europe the gills of this species appear to be very rarely free from this epizoon, and sometimes bear them in great numbers (Fig. 85). *Stylocometes*, Stein, is found on the gills of Asellus aquaticus and, rarely, on the gills of Gammarus and on colonies of *Ophrydium*. It differs from *Dendrocometes* in having more numerous arms (10-12).

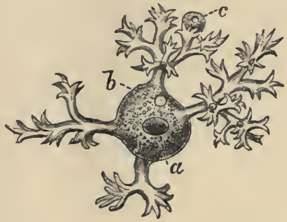

Fig. 85.

*Dendrocometes paradoxus*, Stein. Epizoic on the gill of Gammarus. *a*, meganucleus; *b*, contractile vacuole; *c*, a small organism paralysed and held fast by one of the arms. × 350.

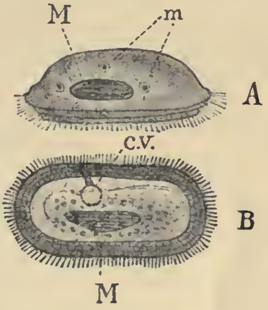

Fig. 86.

Free-swimming gemmulae of *Dendrocometes paradoxus*, Stein, as seen, *A*, from the side, *B*, from below. *M*, meganucleus; *m*, micronuclei; *c.v*, contractile vacuole. (After Bütschli. The micronuclei have been added by the author from original preparations.) × ca. 300.

Family Dendrosomina, Bütschli. Characterised by the lobed or ramified form of the body, each lobe or branch bearing a number of suckers. There is no peduncle. *Trichophrya*, Clap. and L. The body is lobed, ovoid, or hemispherical in shape. It is sometimes attached at one point or disc, but sometimes free and amoeboid. When the body is distinctly lobed the suckers are confined to the free ends of the lobes; in other forms the tentacles are more irregularly scattered. There are nine species, and they are found on the gills of fish (perch and pike), on the abdominal segments of Cyclops, on Epistylis, Conferva, Anacharis, on Salpa, on Algae, Hydroids, etc. *Dendrosoma*, Bütschli. This form (Figs. 32 and 87) reaches to a considerable size, 2·4. In its fully developed condition it consists of a number of long lobes of branches rising from a creeping stolon. There is a continuous axial meganucleus extending throughout the branches of the stolon and the upright lobes. At the extremity of each lobe there is a cluster of delicate suckers. Reproduction is by means of endogenous gemmulae and by external non-ciliated fragments which break off from the lobes and give rise to new individuals. They are found on Anacharis and Myriophyllum.

Family Ophryodendrina, Stein. *Ophryodendron*, Clap. and L. The body is usually oval or columnar in shape. It is fixed at the posterior extremity. With or without a peduncle. At the anterior extremity there are one to four processes of the body provided with numerous styliform tentacles. The animal produces by internal gemmation numerous gemmules with peritrichous cilia. 0·84. Marine. Attached to Hydroids, Algae, and the limbs of Crustacea (Fig. 87).

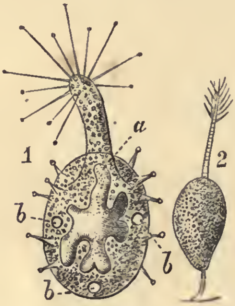

Fig. 87.

1, *Dendrosoma radians*, Ehrb. An early stage in development, with only a single branch springing from the attached gemmula. × 600. For adult colony see Fig. 32, p. 384. 2, *Ophryodendron pedicellatum*, Hincks. × 300.

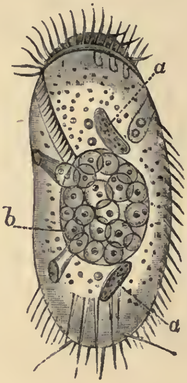

Fig. 88.

A specimen of *Stylonychia mytilus*, containing a cyst of endoparasitic spores (*b*) of *Sphaerophrya pusilla*, Clap. and L. *a*, *a*, the two meganuclei.

Family Hypocomina, Bütschli. Plano-convex in shape, with a single sucker on the ventral side. Numerous cilia on the ventral side. *Hypocoma*, Gruber. 0·046. On the peduncles of various marine Vorticellids.

Family Urnulina, Fraipont. *Rhynceta*, Zenker. (Fig. 13.) Cylindrical in form, with one long sucker. No cilia. 0·09. Freshwater. Attached to the limbs of Cyclops, and the gills of Gammarus. *Urnula*, Clap. and L. Urceolate test. Body oval or spherical. One or two filiform tentacles. Gemmula holotrichous. ·12. On the peduncle of Epistylis plicatilis. *Acinetopsis*, Robin. Cupuliform test attached by a short peduncle. A single flexible tentacle. ·08. On Sertularia.

Family Podophryina. *Podophrya*, Bütschli. Pedunculate. Body spherical, with numerous tentacles scattered over its distal surface. A single gemmula formed at a time. ·08. Freshwater. *Sphaerophrya*, Clap. and L. (Figs. 88 and 89.) Non-pedunculate. Spherical in form. Numerous scattered suckers. Sometimes endoparasitic on Paramoecium, Stylonychia, etc. ·08. Freshwater. *Endosphaera*, Engelmann. Life-history little known, but in adult stage probably wholly endoparasitic on

Vorticellids and Acinetaria. *Amoebophrya*, Köppen. (Fig. 90.) With a circlet of tentacles and a spiral groove provided with cilia in the free

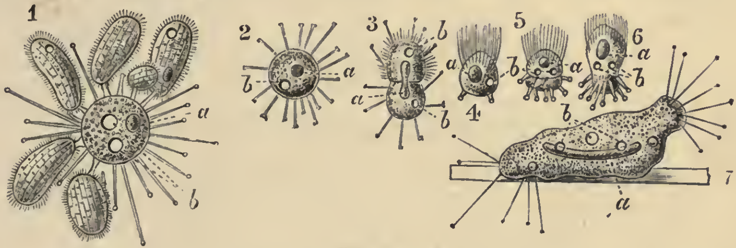

FIG. 89.

1, *Sphaerophrya magna*, Maupas. × 300. It has seized with its suckers, and is in the act of sucking out the juices of six examples of Colpoda parvifrons. *a*, meganucleus; *b*, contractile vacuoles. 2, *Sphaerophrya urostylae*, Maupas. × 200. Normal adult. *a*, meganucleus; *b*, contractile vacuoles. 3, the same dividing by transverse fission, the anterior moiety with temporarily developed cilia. 4, 5, 6, *Sphaerophrya stentorea*, Maupas. × 200. Parasitic in Stentor, and at one time mistaken for its young. 7, *Trichophrya epistylides*, Cl. and L. *a*, meganucleus; *b*, contractile vacuoles.

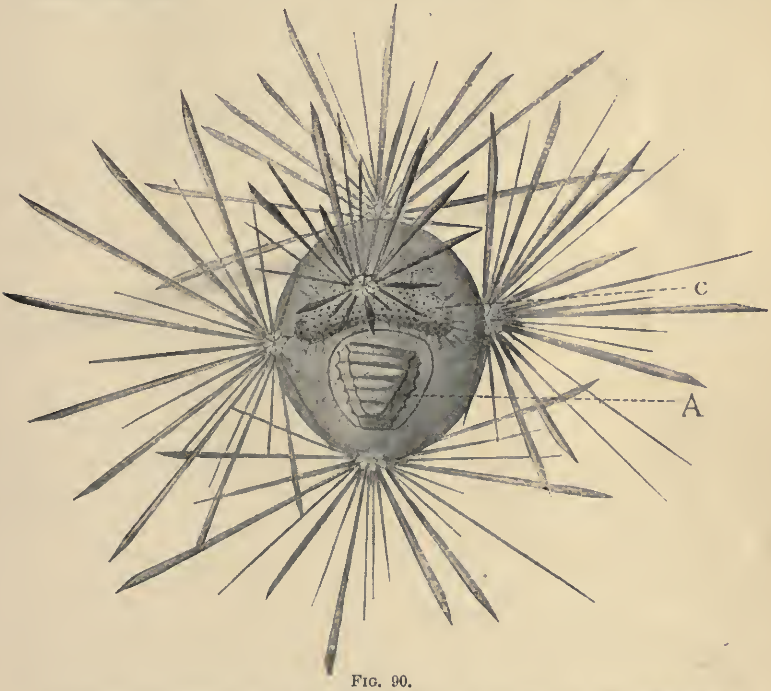

FIG. 90.

*Amoebophrya sticholonchae* (at *A*) encysted in the protoplasm of the Acanthometrid Sticholonche zanclea. *C*, central capsule of the Sticholonche. (After Borgert.) × 260.

state. Without cilia or tentacles in the parasitic stage. Endoparasitic in Acanthometra and Sticholonche.

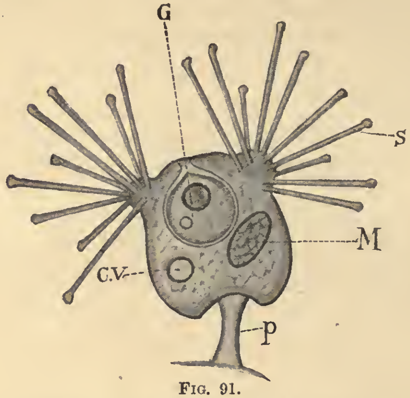

FIG. 91.

*Tokophrya cyclopum*, Cl. and L. *M*, meganucleus; *p*, pedicle; *c.v*, contractile vacuole; *G*, gemmula in brood chamber; *S*, groups of suckers. (After Schewiakoff.) × 1000.

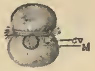

FIG. 92.

Gemmula of *Tokophrya cyclopum*, Cl. and L., ×750, with an equatorial band of cilia. *M*, meganucleus; *c.v*, contractile vacuole. (After Schewiakoff.)

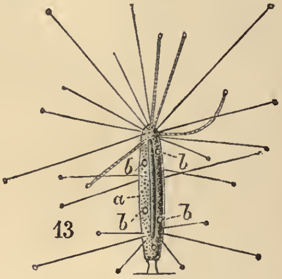

FIG. 93.

*Tokophrya elongata*, Clap. and L. *a*, meganucleus; *b*, *b*, contractile vacuoles. × 150.

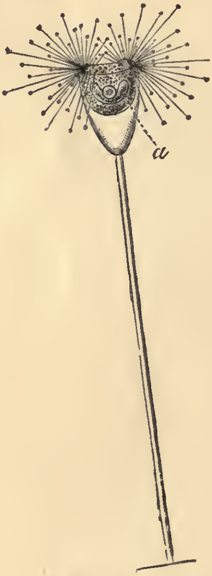

FIG. 94.

*Acineta grandis*, Kent, × 100, showing pedunculated lorica and disc with two bunches of suckers. *a*, meganucleus.

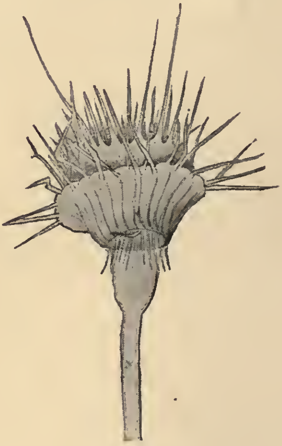

FIG. 95.

A single head of a species of *Ephelota*, with three whorls of tentacles. (After Ishikawa.) The individual is ·5 mm. × ·16 mm. in size.

Family METACINETINA, Bütschli. *Metacineta*, Bütschli. Body capable of being completely retracted into the conically expanded termination of the peduncle. 0·7. Freshwater.

Family Acinetina, Bütschli. *Hallezia*, Sand. Animal attached by a small protoplasmic knob. Numerous suckers at the anterior extremity. Several endogenous gemmules formed at one time. ·18. Freshwater. *Tokophrya*, Bütschli. (Figs. 91, 92, 93.) Pedunculate, but with the saucer-shaped terminal expansion absent or slightly developed. Suckers fasciculate or dispersed. Endogenous gemmation. ·25. Freshwater and marine. *Acineta*, Ehrb. (Fig. 94.) Pedunculate, with well-marked terminal expansion of the peduncle. ·3. Marine and freshwater. *Solenophrya*, Clap. and L. With terminal expansion of the peduncle globular in form.

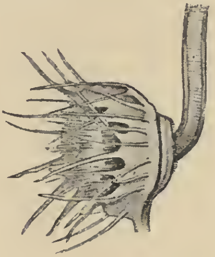

Fig. 96.

A single gemmula of a species of *Ephelota*, showing on the right a small disc of cilia mounted on the end of a long stalk. (After Ishikawa.)

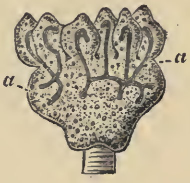

Fig. 97.

*Ephelota* (Hemiophrya) *gemmipara*, Hertwig. Example with six gemmulae in process of formation, into each of which a branch of the meganucleus ($a$, $a$) is extended. (After Hertwig.) × 400.

Family Ephelotina, Sand. *Ephelota*, Wright. Tentacles and suckers on the anterior surface. Reproduction by multiple exogenous gemmulae (Figs. 21, 34, 97). No terminal expansion of the peduncle. ·25. Marine. *Podocyathus*, Kent. Small conical expansion at the summit of the peduncle. Reproduction by one or two small tentaculate gemmulae. ·05. On marine Bryozoa and on Campanularia.

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*Doflein, F.* Studien zur Naturgeschichte der Protozoen—I. *Kentrochona nebaliae;* II. *Kentrochonopsis multipara.* Zool. Jahrb. 10.

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*Wallengren, H.* Ueber die totale Konjugation bei Vorticellina. Biol. Centralbl. xix.

### ADDENDUM.

*Roux, J.* Faune infusorienne des Environs de Genève, 1902.

# INDEX

To names of Families, Sub-Families, and Genera; to technical terms; and to names of Authors discussed in the text.

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